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Fishery Bulletin

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Contents

Articles

391–403 **Allman, Robert J., and Churchill B. Grimes**
Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures

404–413 **Anderson, Todd W., Claudine T. Bartels, Mark A. Hixon, Erich Bartels, Mark H. Carr, and Jonathan M. Shenker**
Current velocity and catch efficiency in sampling settlement-stage larvae of coral-reef fishes

414–422 **Boje, Jesper**
Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies

Companion papers

423–433 **Browne, Patience, Jeffrey L. Laake, and Robert L. DeLong**
Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples

434–447 **Laake, Jeffrey L., Patience Browne, Robert L. DeLong, and Harriet R. Huber**
Pinniped diet composition: a comparison of estimation models

448–465 **Davis, Tim L. O., and Clive A. Stanley**
Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight observed with ultrasonic telemetry

466–474 **Epperly, Sheryan P., and Wendy G. Teas**
Turtle excluder devices–Are the escape openings large enough?

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475–490 **Gibbons, Mark J., André J. J. Goosen, and Patti A. Wickens**
Habitat use by demersal nekton on the continental shelf in the Benguela ecosystem, southern Africa

491–509 **Gold, John R., Elena Pak, and Doug A. DeVries**
Population structure of king mackerel (*Scomberomorus cavalla*) around peninsular Florida, as revealed by microsatellite DNA

510–518 **Hazell. R. W. Anthony, David S. Schoeman, and Mark N. Noffke**
Do fluctuations in the somatic growth rate of rock lobster (*Jasus lalandii*) encompass all size classes? A re-assessment of juvenile growth

519–536 **Jacobson, Larry D., and Steven X. Cadrin**
Stock-rebuilding time isopleths and constant-*F* stock-rebuilding plans for overfished stocks

537–544 **McDowell, Jan R., and John E. Graves**
Nuclear and mitochondrial DNA markers for specific identification of istiophorid and xiphiid billfishes

545–558 **McGarvey, Richard, and Anthony J. Fowler**
Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest

559–581 **Mueter, Franz J., and Brenda L. Norcross**
Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska

582–592 **Nelson, Gary A.**
Age, growth, mortality, and distribution of pinfish (*Lagodon rhomboides*) in Tampa Bay and adjacent Gulf of Mexico waters

593–608 **Overholtz, William J., and Kevin D. Friedland**
Recovery of the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex: perspectives based on bottom trawl survey data

609–623 **Warlen, Stanley M., Kenneth W. Able, and Elisabeth Laban**
Recruitment of larval Atlantic menhaden (*Brevoortia tyrannus*) to North Carolina and New Jersey estuaries: evidence for larval transport northward along the east coast of the United States

624–631 **Witzell, Wayne N., Anna L. Bass, Michael J. Bresette, David A. Singewald, and Jonathan C. Gorham**
Origin of immature loggerhead sea turtles (*Caretta caretta*) at Hutchinson Island, Florida: evidence from mtDNA markers

Notes

632–640 **Bilkovic, Donna Marie, John E. Olney, and Carl H. Hershner**
Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) in the Mattaponi and Pamunkey Rivers, Virginia

641–647 **McBride, Richard S.**
Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*)

648 *Errata*

649 *Subscription form*

Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures

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Abstract–The goal of our study was to understand the spatial and temporal variation in spawning and settlement of gray snapper (*Lutjanus griseus*) along the West Florida shelf (WFS). Juvenile gray snapper were collected over two consecutive years from seagrass meadows with a benthic scrape and otter trawl. Spawning, settlement, and growth patterns were compared across three sampling regions (Panhandle, Big bend, and Southwest) by using otolith microstructure. Histology of adult gonads was also used for an independent estimate of spawning time. Daily growth increments were visible in the lapilli of snapper 11–150 mm standard length; ages ranged from 38 to 229 days and estimated average planktonic larval duration was 25 days. Estimated growth rates ranged from 0.60 to 1.02 mm/d and did not differ among the three sampling regions, but did differ across sampling years. Back-calculated fertilization dates from otoliths indicated that juveniles in the Panhandle and Big Bend were mainly summer spawned fish, whereas Southwest juveniles had winter and summer fertilization dates. Settlement occurred during summer both years and in the winter of 1997 for the southern portion of the WFS. Moon phase did not appear to be strongly correlated with fertilization or settlement. Histological samples of gonads from adults collected near the juvenile sampling areas indicated a summer spawning period.

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Fish. Bull. 100:391–403 (2002).

A primary goal of fisheries ecology is to determine the causes of annual variation in recruitment and to predict the number of individuals that reach a harvestable size (Frank and Leggett, 1994). This variation can be substantial; recruitment to marine fish stocks can vary by one or two orders of magnitude (Shepherd and Cushing, 1990). An understanding of recruitment dynamics remains a critical, unresolved problem in fisheries science (Houde, 1987). Improved understanding is vital for better conservation of exploited marine fish populations for it would enable prediction of future harvests (Wooster and Bailey, 1987).

Gray snapper (*Lutjanus griseus*), also known as mangrove snapper, are found in the western Atlantic and Gulf of Mexico from North Carolina to Bermuda and south to Brazil. Rarely, individuals are recorded as far north as New England (Hoese and Moore, 1977). Adults generally occur offshore in areas associated with coral reefs or other hard bottom substrate. Spawning off Florida is thought to occur from June through September, and individual gray snapper probably spawn more than once during the spawning season (Starck, 1971). Larvae, which are planktonic up to about 10 mm standard length (SL) (Starck, 1971), have been reared in the laboratory and described by Richards and Saksena (1980). Juvenile gray snapper are associated with inshore *Thalassia* beds (Chester and Thayer, 1990). Young snapper remain in these *Thalassia* beds until approximately 80 mm SL when they begin to congregate around debris and channel edges. Sexual maturity occurs at 175–180 mm or three years of age (Starck, 1971).

Gray snapper support an important recreational and commercial fishery in the Gulf of Mexico. Commercial landings in the Gulf of Mexico, once over 900,000 lb in 1983 had declined to less than 430,000 lb by 1997 (Bennett[1]). Gray snapper are popular among sport fishermen; recreational landings in the Gulf of Mexico for 1997 were estimated at 877,000 lb (U.S. Dep. Commer.[2]).

The boundaries of the study area approximately represent the range of seagrass meadows along the West Florida shelf (WFS) (i.e. St. Andrew Bay is near the northwest extreme and Ft. Myers is near the southwest). The study area also experiences variation in climate, the north portion being warm-temper-

[1] Bennett, J. 1998. Automated landings assessment for responsive management. Gulf of Mexico Commercial landings for selected species, 87 p. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, Miami, FL 33149.

[2] U.S. Department of Commerce. 1998. Fisheries of the United States. 1997. Current fishery statistics no. 9700, 156 p. Statistics Div, Rm 12340, 1315 East-West Highway, Silver Spring, MD 20910-3282.

ate and the southmost boundary being semitropical (Zieman and Zieman, 1989). This climate change results in latitudinal variation in the shallow water communities along the WFS: from a mainly West Indian fauna in the south to a Carolinian fauna in the north (Smith, 1976; Lyons, 1979).

The goal of our study was to improve our understanding of the recruitment dynamics of gray snapper by determining the spatial and temporal patterns in spawning and settlement along the WFS. The objectives of this study were 1) to establish spawning time through otolith back-calculation and the examination of adult gonads, 2) to determine settlement time (i.e. planktonic larval duration) from otolith microstructure, 3) to estimate growth rates for juvenile gray snapper, 4) to compare estimated spawning times, settlement times, and growth rates between sampling regions and years, and 5) to examine the potential influence of lunar phase on spawning and settlement events.

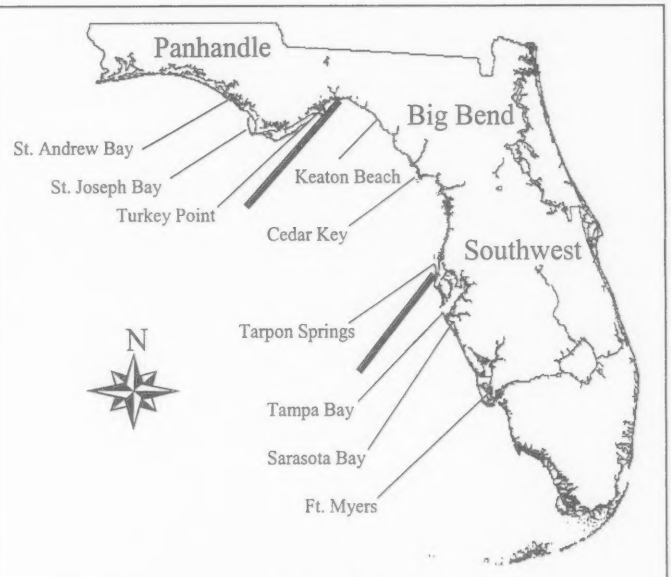

Figure 1

Sampling regions and station locations along the West Florida shelf (WFS). Thick black lines demarcate the three sampling regions: region 1, the Florida Panhandle; region 2, Big Bend; and region 3, Southwest Florida.

Materials and methods

Sampling and collection

We collected juvenile reef fish from the seagrass beds of the WFS from St. Andrew Bay in northwest Florida to Ft. Myers in southwest Florida. For spatial comparison of the results, we divided the study area into three sampling regions chosen on the basis of the differences in faunal composition (Lyons and Collard, 1974; Smith, 1976; Hoese and Moore, 1977) and type of coastal environment (Price, 1954) (Fig. 1). Region 1, the Florida Panhandle, embraces St. Andrew Bay to the St. Marks River, an area of sand beaches and barrier islands. Region 2, the Big Bend, spans the area from the St. Marks River south to Tarpon Springs. The Big Bend is unlike the other regions in that it has no barrier islands and is considered a zero-energy coastline (Murali, 1982). Region 3, Southwest Florida, includes the area from Tarpon Springs south to Ft. Myers. This region is similar to region 1 in that it is composed largely of sand beaches and barrier islands (Zieman and Zieman, 1989).

Station locations within these regions were chosen according to abundance of economically important fin fish species (Koenig and Coleman[3]). The 20 stations were located where there were large dense areas of seagrass in close proximity to the open gulf. The dominant species of seagrass in the study area is turtle-grass, *Thalassia testudinum*, followed by manatee-grass, *Syringodium filiforme*, and shoal-grass, *Halodule wrightii* (Zieman and Zieman, 1989). Station depth generally ranged from 1 to 3 meters.

We collected juvenile fish for this study every other month in 1996 and 1997, beginning in late February of 1996 and early March of 1997. At each station we made five replicate tows of 150 meters (m) in approximately 5 minutes (1.8 km/hour) using two different types of trawls. To collect the smallest postsettlement juveniles, a 1-m by 0.40-m benthic scrape constructed of a stainless steel frame with a 2-mm nylon mesh tail bag was used. This trawl was used from the beginning of the year until the fall. We used a 5-m by 3-m otter trawl with a 3-mm nylon mesh tail bag to collect larger individuals year round. The contents of each trawl were sorted and all juvenile fish of commercial value were removed, bagged, and stored on ice. At the end of a sampling trip, all juvenile fish collected were frozen. In the laboratory juvenile gray snapper were removed from samples, thawed, measured (standard length [SL] to the nearest 0.1 mm), and weighed to the nearest 0.1 g.

Otolith preparation and interpretation

Both the sagittae and lapilli were extracted from each snapper under a dissecting microscope by the "open-the-hatch method" (Secor et al., 1992). One lapillus was chosen at random from each fish for measurement. Whole lapilli were viewed with a compound microscope at 50× magnification with a video camera and monitor and the image was digitized on a microcomputer with image analysis software (BioScan, 1990). A measurement (nearest μm)

[3] Koenig, C. C., and F. C. Coleman. 1998. Recruitment indices and seagrass habitat relationships of the early juvenile stages of gag, gray snapper, and other economically important reef fishes in the eastern Gulf of Mexico. Final report (MARFIN award no. NA57FF0055) to Florida State University, 66 p. Department of Biological Sciences, The Florida State Univ., Tallahassee, FL 32306-2043.

was made from the anterior edge to the posterior edge along the longest axis.

We computed the linear regression of standard length on lapillus length to determine if otolith growth and somatic growth were proportional. To prepare lapilli for age determination, both lateral surfaces of the otolith were ground and polished on glass plates covered with a 3600- and 6000-grit polishing cloth. After being polished, the lapillus was mounted on a microscope slide with Pro-texx® mounting medium. Thirteen sagittae were also prepared to determine if sagittal section counts were consistent with lapilli counts. Because of the concave-convex shape of the sagittae, the technique used for examining the lapillus was not possible. Therefore, the more labor intensive process of embedding and sectioning the whole sagittae had to be used (Secor et al., 1992).

Growth in mm/day was estimated as the slope of the linear regression of standard length on the number of daily increments in the lapillus. Analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were used to determine if estimated growth rates varied significantly among sampling regions and years.

Increment counts were made from sections of the lapilli and sagittae by using a compound microscope at 400–1000× magnification. Oil immersion was used at the 1000× magnification. Daily increments were distinguished from subdaily increments with the method of Campana (1992). Increments were counted twice by the same reader and counts that were different by no greater than 5% were averaged. Increment counts that differed by more than 5% were counted a third time, and if the third count differed by more than 5% of the previous counts, the otolith was rejected. An increment correction (3 days) was added to the total number counted based on the assumption that the first increment was not formed until after first feeding (i.e. approximately 3 days after fertilization) (Lindeman, 1997; Lindeman et al., 2000). This corrected increment count was subtracted from capture date to determine the fertilization date.

We interpreted the settlement mark in the lapillus to be where the pattern in the increment widths changed markedly (Wellington and Victor, 1989). Increments were counted from the primordium to the settlement mark and a correction of three increments was added to estimate the number of days before settlement or the planktonic larval duration. Those lapilli that did not have an obvious settlement mark were excluded from the analysis. Settlement dates were calculated by subtracting the number of post-settlement increments from the date of capture. ANOVA was used to compare the age at settlement (i.e. planktonic larval duration) with region, year, and region-year interaction. After converting lunar day of fertilization or settlement to a circular scale (Zar, 1984), we used a chi-square test to determine if fertilization and settlement dates were uniformly distributed across the lunar month.

To validate the periodicity of increment formation in lapilli we conducted an otolith marking experiment. Lapilli of live fish were marked with alizarin complexone, which has been shown to produce a well-defined mark in the otoliths of juvenile fish without producing high mortality (Tsukamoto et al., 1989; Lang and Buxton, 1993). Approximately 30 juveniles were captured with a benthic trawl and held in an 800-gallon flow-through seawater system for several days so that they might acclimate to captivity. Juveniles were fed once daily *ad libitum*. Because of the photosensitivity of alizarin complexone, juveniles were immersed in 20 L of an aerated 200 mg/L solution of alizarin complexone for 24 h in the dark. Juveniles were removed from the solution and returned to the flow-through seawater tank. Juveniles were sacrificed 7, 14, 21, or 28 days after marking and their lapilli were removed and prepared as previously described. Increments deposited after the alizarin complexone mark were counted as previously described, except that transmitted ultraviolet light was used to read increments. Linear regression was used to compare number of increments counted after the alizarin-complexone mark in the lapillus to the number of days the juveniles were held after marking. A *t*-test was used to determine if the slope of this regression was significantly different from 1.0.

Gonad histology and analysis

To obtain an estimate of the spawning time that was independent of otolith-based spawning dates, adult gray snapper gonads were examined. All adult gray snapper were collected as part of an ongoing study by the National Marine Fisheries Service on reef fish reproduction. Fish were collected from commercial and recreational landings from Panama City, Florida, to Ft. Myers, Florida, from January to December in 1996 and from April to November in 1997. Each fish was weighed whole (i.e. ungutted [g]) and total length (TL) and fork length were measured (mm). All fish collected were at least 252 mm TL (minimum legal size) and were assumed to be sexually mature (Domeier et al., 1996).

Gonads were removed and stored on ice and then processed by the methods of Collins et al. (1996). A small sample of each gonad was examined with a dissecting microscope (250×) to measure the maximum oocyte diameter (nearest 0.1 mm). The developmental stage of ovarian sections was determined by using the methods of Wallace and Selman (1981). Ovarian stages were assigned on the basis of the most advanced ovarian stage or follicle stage present: 1—primary growth (early oocytes); 2—cortical alveolar (previtellogenic); 3—vitellogenic; 4—hydrated; and 5—spent (i.e. presence of postovulatory follicles). Sections of testes were staged according to the methods of Moe (1969): 1—spermatogonia; 2—primary spermatocytes; 3—secondary spermatocytes; 4—spermatids; and 5—spermatozoans. The timing and duration of spawning were determined by plotting oocyte diameter and histological development stage by sampling date.

Results

Sampling and collection

Juvenile gray snapper were found in seagrass meadows along the west Florida shelf from June to November in the two most northern sampling regions, and from April

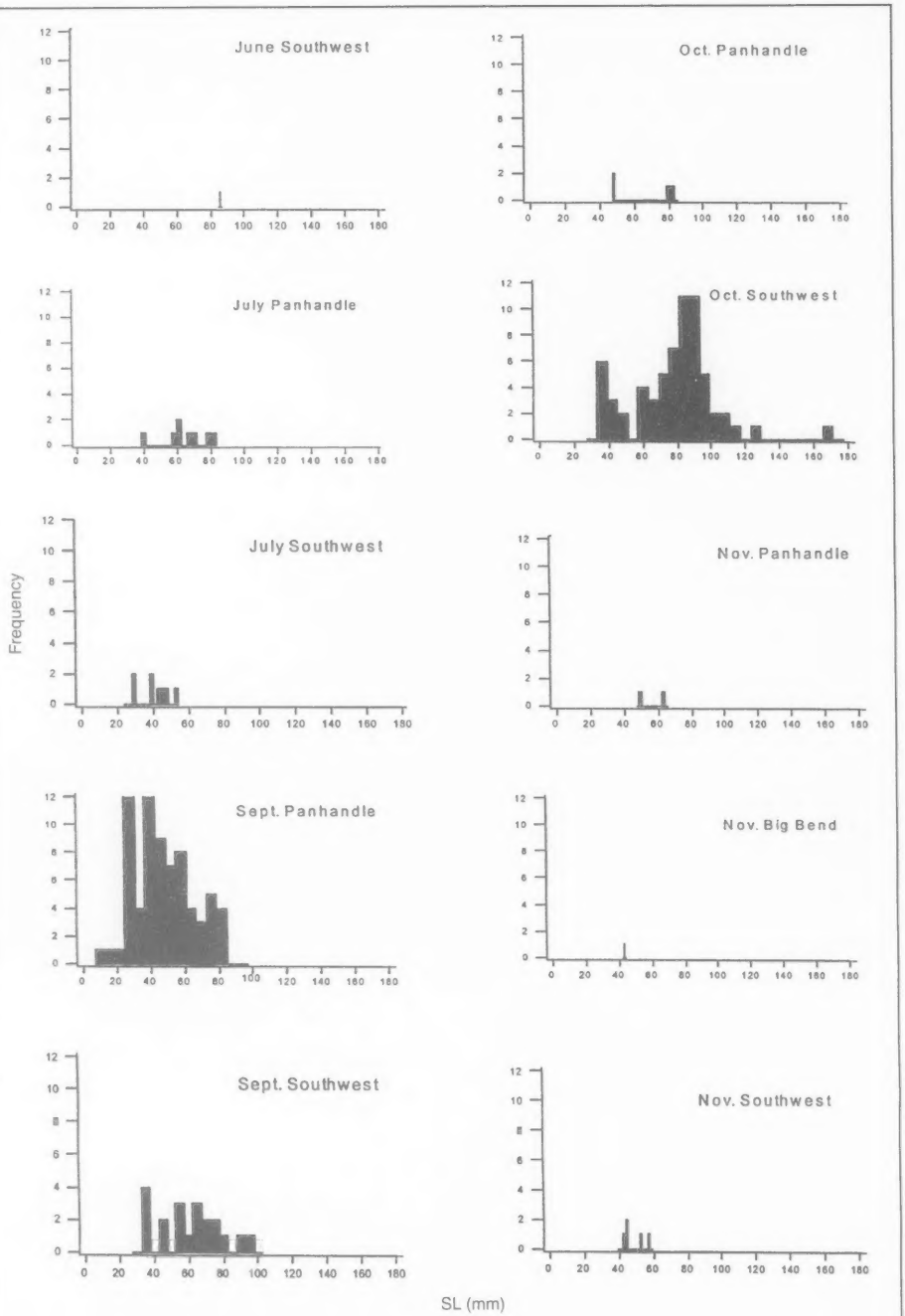

Figure 2

Length (SL, mm) frequency distribution of gray snapper juveniles by region and sampling month in 1996.

to November in the most southern area. The first juvenile was collected in the otter trawl in June 1996 from the Southwest (Fig. 2). In July we collected 14 fish in the benthic scrape and only one in the otter trawl along the entire WFS. The largest numbers were collected in September and October from the Panhandle and Southwest. The fol-

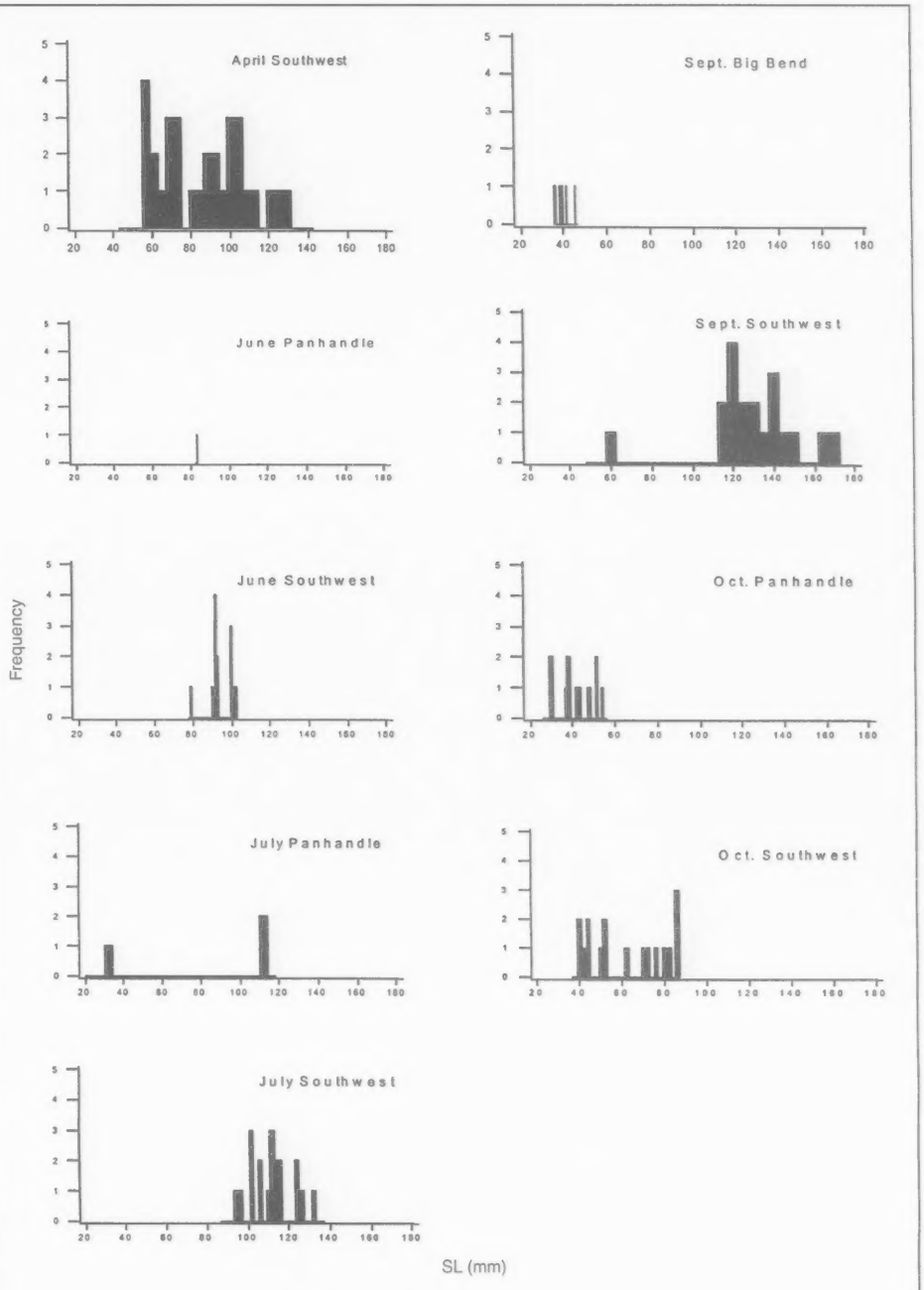

Figure 3

Length (SL, mm) frequency distribution of gray snapper juveniles by region and sampling month in 1997.

lowing year (1997), juveniles were initially collected in April in the otter trawl in the most southerly part of the Southwest sampling area (i.e. near Sanibel Island) (Fig. 3). The catch rate decreased in June, then increased during late summer, and peaked in September. Only two fish were collected in the benthic scrape, both in June.

There was evidence of multiple cohorts in the Southwest in October 1996 and in April 1997. Juveniles collected in 1997 (mean=88.3 mm SL) were, on average, about 50% larger than those collected in 1996 (mean=59.9 mm SL). Fish collected from the Southwest were also larger on average than those from the Panhandle both years.

Age and growth

Increments in the lapillus occurred at regular intervals and a consistent width and marked contrast was evident between each one. More closely spaced increments occurred at irregular intervals with less contrast between them. Usually we counted fewer increments in sagittae than in lapilli. Lapilli were thinner and flatter than sagittae and therefore required less grinding and could be examined whole, whereas sagittae had to be sectioned first. Increments near the edge of the lapilli were also clearer and easier to distinguish compared with those from sagittal sections. Increment counts were successfully assigned to 137 (71%) of the juveniles collected in 1996 and 97 (82%) of the 1997 collection. Uncorrected increment counts ranged from 35–128 (mean=75) in 1996 and 50–226 (mean=125) in 1997.

Several lines of evidence suggested that increments were deposited daily. The linear regression of SL (mm) on lapillus length (μm) indicated a highly significant relationship between body size and otolith size for fish collected in 1996 ($P<0.000$, $r^2=0.97$) and 1997 ($P<0.000$, $r^2=0.96$). Juveniles selected for the otolith marking experiment ranged from 31.4 to 44.6 mm SL (mean=38.4 mm, standard error=0.63 mm). Only 21 out of 30 surviving alizarin-complexone–marked juveniles had otoliths with visible marks and no fish harvested on day 21 had readable marks. Mean growth rate for survivors was estimated at 0.33 mm/d. The slope ($b=0.87$) of the regression of the number of increments counted after the alizarin mark on the number of days juveniles were held after marking was not significantly different from 1.0 (Fig. 4) (t-test, $P<0.05$); therefore we did not reject the hypothesis that increments were deposited daily.

Instantaneous daily growth of juvenile snapper was 1.02 mm/d in 1996 compared with 0.60 mm/d in 1997 (Fig. 5). ANOVA indicated a significant difference in slopes (i.e. growth rates) between years ($P<0.001$). However, ANCOVA indicated that there was no significant difference in growth rate among regions. Because there was a significant difference in standard lengths between years and regions, only those size ranges that overlapped between the two regions (i.e. Panhandle and Southwest, 1996: 29–83 mm SL, 1997: 39–112 mm SL) and between years (i.e. 32–110 mm SL) were included in the analysis.

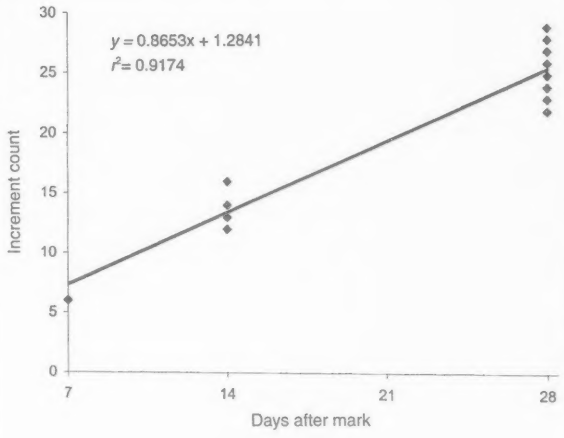

Figure 4

Linear regression of increment count on number of days after alizarin marking of the lapillus.

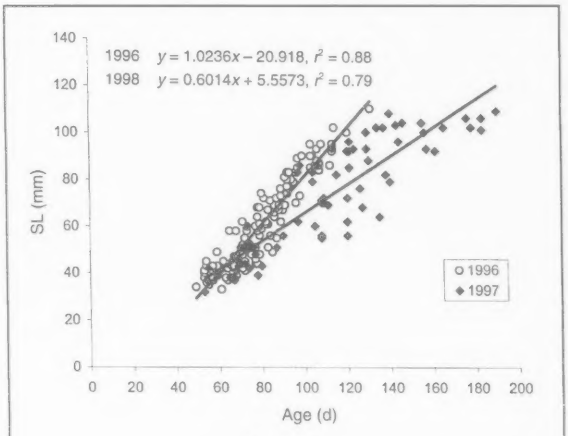

Figure 5

Linear regression of SL (mm) on age (d) for 1996 and 1997.

Fertilization-date distribution

There were distinct patterns in the temporal and spatial distribution of fertilization dates. Our results however provided little support for lunar periodicity in spawning. Back-calculated fertilization dates indicated that surviving juveniles in the Panhandle and Big Bend were mainly summer spawned fish, whereas Southwest juveniles had winter and summer fertilization dates. In 1996, the earliest back-calculated birth date was 25 February from a fish from the Southwest, although a few (i.e. six fish) were recorded from late April and early May from the Panhandle and a few more by mid-May from the Southwest (Fig. 6). Most fish spawned beginning in mid-June and a peak in fertilization dates occurred during mid-July for both regions. Frequency of spawning then declined and the latest fertilization date of the year was recorded in mid-September from the Southwest. A chi-

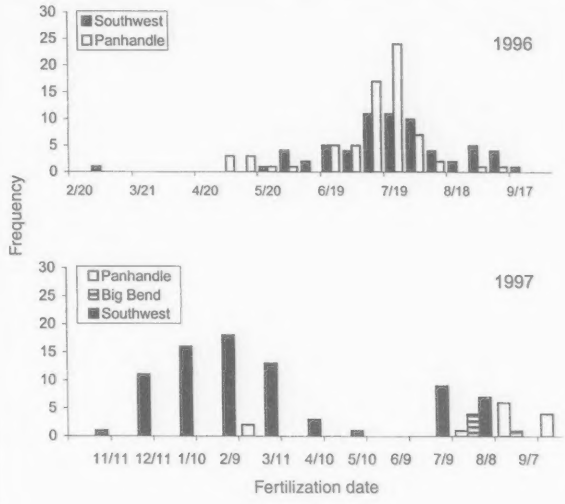

Figure 6

Fertilization-date distribution for 1996 and 1997.

square test revealed only a marginal difference ($P<0.10$) from a uniform distribution in fertilization dates across lunar month.

As in 1996, fertilization in 1997 began in mid-June, peaked in early August, and included birth dates from all three regions; however, the distribution for 1997 was bimodal. Spawning began in November of 1996 and peaked in late January of 1997, then declined into April. With the exception of two individuals collected in late February from the Panhandle, all individuals from the first fertilization-date peak were from the Southwest. The last back-calculated fertilization date for the year was in early September from the Panhandle. Fertilization dates for 1997 did not conform to a lunar cycle because a chi-square test indicated no significant difference from a uniform fertilization-date distribution across lunar month.

Results from the reproductive condition of adult gonads were compared with results from back-calculated fertilization dates from otoliths to determine if surviving juveniles were derived from a subset of the original propagules. We compared otolith data with oocyte diameters because large ova are indicative of ripe females (i.e. >0.59 mm maximum oocyte diameter) (Davis and West, 1993). In 1996, the maximum oocyte diameter distribution indicated that females were in spawning condition from May to September and that a peak in spawning activity occurred in mid-July (Fig. 7). Spawning activity, signified by the presence of hydrated oocytes, also occurred from May through mid-September. Only one female with postovulatory follicles was found in 1996, collected in mid-July. Male spawning times (i.e. May–September) mirrored those of females; however, only five males contained ripening spermatids, and none contained spermatozoa in 1996. All gonads collected in 1996 were from the Panhandle.

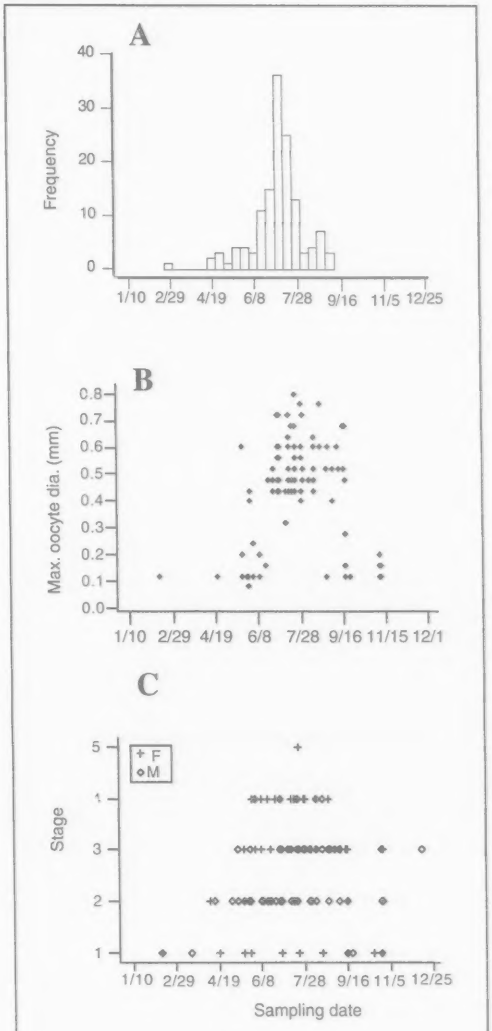

Figure 7

Comparison of spawning time as determined by back-calculation from otoliths (**A**), maximum oocyte diameter (**B**) and histological stage (**C**) for 1996. All fish were collected from the Panhandle.

In 1997 gonad data were available from all three regions and the results of comparisons of gonads from the three regions may indicate the presence of juveniles that were not derived from local spawning. Gonad data for all regions indicated peak spawning during mid-July (Fig. 8). Gonad data from the Panhandle suggested spawning times similar to those for the otolith data, i.e. a May through September spawning period and a summer peak. However, the back-calculated fertilization dates from late February and early March did not correspond to oocyte diameter or histological-stage data. Very few juveniles

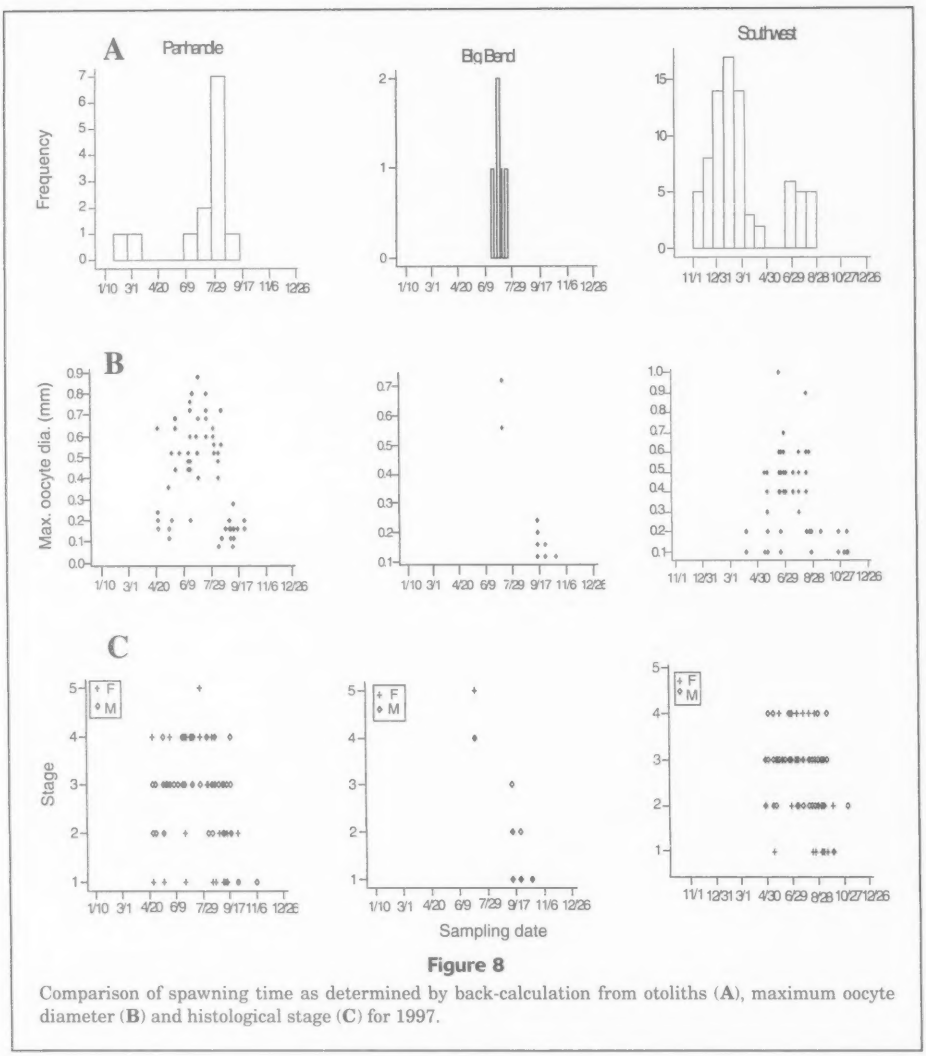

Figure 8

Comparison of spawning time as determined by back-calculation from otoliths (**A**), maximum oocyte diameter (**B**) and histological stage (**C**) for 1997.

or adult fish were collected from the Big Bend; however, these data also suggested a mid-summer spawning period. Oocyte diameter and developmental stage data from the Southwest indicated summer spawning (May to September) but because no adult gonads were collected earlier in the year, a winter fertilization-date mode (as back-calculated from otoliths) could not be determined.

Larval duration

Presumed settlement marks were distinguishable in some, but not all otoliths that were assigned ages. These marks were identified by a sharper contrast than preceding marks (Fig. 9). In addition, at this mark the increment pattern changed abruptly, postsettlement increment widths being consistently narrower than those laid down before settlement. Of the 135 otoliths collected during 1996 which were assigned ages, 80 (59%) had readily distinguishable settlement marks, whereas in 1997, 62 (64%) had distinguishable marks. The estimated age at settlement (planktonic larval duration) for 1996 and 1997 fish ranged from 20 to 32 days (mean=25 days) and from 20 to 33 days (mean=24.7 days), respectively. ANOVA indicated no significant sampling region or year effect or region-and-year interaction on the age at settlement (planktonic larval duration).

In 1996, settlement first began in mid May in the Panhandle and continued throughout the summer, peaking during the first week of August in the Panhandle and Southwest, and ending finally on 1 October in the Southwest (Fig. 10). Results for settlement date data showed no evidence for lunar periodicity in settlement, a chi-square

test indicating that the distribution of lunar settlement dates was not significantly different from a uniform distribution. The back-calculated settlement date distribution for 1997 indicated two distinct settlement events. Settlement of the first mode began in December of 1996, peaked in late winter, and then declined into late spring. All juveniles from the first event were from the Southwest. The second settlement mode was similar to that seen in the 1996 settlement date distribution, beginning in late June, peaking in early August, and finally ending in the early fall. The evidence for lunar periodicity in settlement in 1997 was weak; a chi-square test indicated only a marginally significant difference ($P<0.10$) from a uniform distribution across lunar month for 1997 settlement dates.

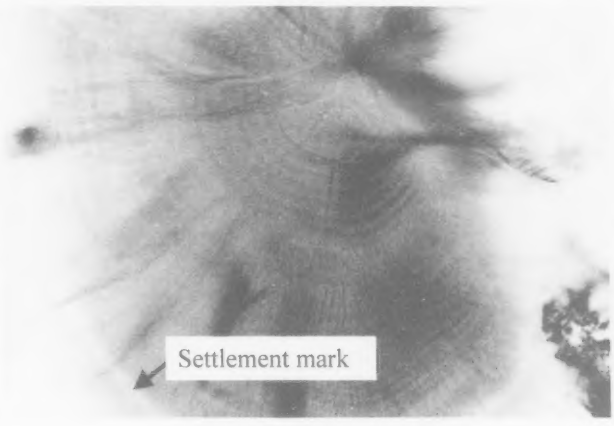

Figure 9
Photomicrograph (400×) of settlement mark in a lapillus of gray snapper.

Discussion

Sampling and collection

The collection of juvenile gray snapper from June to November in 1996 was consistent with a May–September spawning period found from previous studies in which the reproductive condition of adults collected off South Florida was used (Starck, 1971; Domeier et al., 1996). However, in 1997 juvenile gray snapper were initially collected in April from southwest Florida, indicating a much earlier spawning time. Differences in the timing of the first appearance of juvenile snapper for 1997 could be related to the seasonal cycle of seagrass dieback and regeneration. *Thalassia* experiences leaf die off with temperatures below 15°C (Zimmerman and Livingston, 1976). In the northern most part of the sampling region, greater leaf die off and slower growth during the spring would be expected compared with more southerly areas. This would most certainly limit the chances of survival of early settling larvae in the north because of greater predation risk and lower food availability.

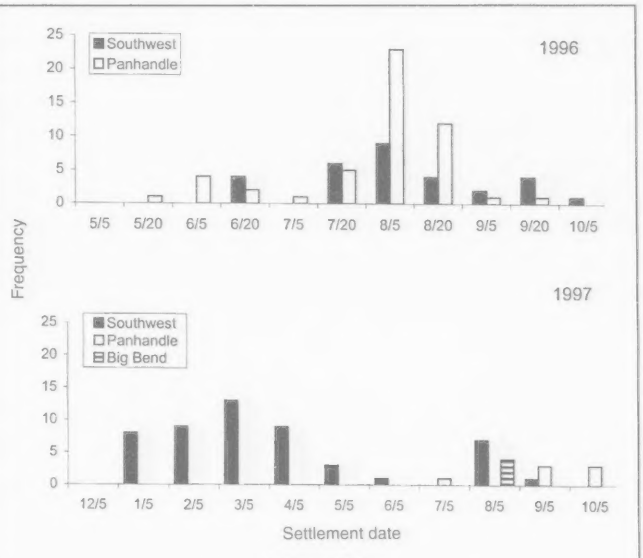

Figure 10
Settlement-date distribution for 1996 and 1997.

If gray snapper are truly recruitment-limited and if postsettlement mortality is relatively constant (Shulman and Ogden, 1987) and individuals do not migrate out of the area during the monitoring period (Robertson et al., 1988), juvenile abundance would be an effective predictor of adult abundance two to three years later when the adults are entering the fishery. Gag (*Mycteroperca microlepis*), a species with a similar early life history to that of the gray snapper, have a low rate of emigration from the seagrass nursery area during summer and a mortality rate of less than 1%/d (Koenig and Coleman, 1998). Johnson and Koenig (in press) found a strong correlation between juvenile gag abundance in seagrass meadows and year-class strength in the fishery several years later. Juvenile indices have been used successfully to document recruitment for a number of temperate fish species and invertebrates. For example, juvenile indices for striped bass were found to explain 83% of the variation in reported landings from 1963 to 1983 (Goodyear, 1985). These data for gray snapper could provide a fishery-independent method for forecasting size of year classes several years into the future. This would be a valuable addition to stock assessment which typically features age-based hind-casting methods such as

virtual population analysis from fishery-dependent data. However, before these data can be used reliably there must be a demonstrated relationship between juvenile abundance and year-class strength.

Age and growth

Because of the strong linear relationship between otolith size and fish size and the regression of increments deposited after alizarin marks on days after marking, we did not reject the hypothesis that one increment was deposited daily. In addition, Ahrenholz (2000) found no significant difference from 1 increment/d deposited from lapilli of alizarin-marked juvenile gray snapper. Juvenile congeneric red snapper (*Lutjanus campechanus*) have also been shown to deposit daily increments above a minimum growth rate (i.e. >0.3 mm/d FL) (Szedlmayer, 1998).

The daily growth rate for juveniles varied between sampling years (1 mm/d in 1996 and 0.6 mm/d in 1997) and was similar to growth rates for juvenile red snapper (0.54–0.86 mm/d, Szedlmayer and Conti, 1999). The difference in growth between years could be explained by the fact that most juveniles collected in 1997 were winter-spawned fish collected from SW Florida that may have experienced lower temperatures and that initially had a slower growth rate. Variability in the growth of larval and juvenile fish has been linked to water temperature in many species (Lang et al., 1994; Nixon and Jones, 1997). However, when the same size range of juveniles was compared between regions, there was no significant difference in growth rate. Similarly there was no difference in regional growth rate of co-occurring juvenile gag from the west Florida shelf (Fitzhugh[4]).

Fertilization-date distribution

All indicators of the temporal distribution of spawning (i.e. juvenile otoliths, oocyte diameter, and histological stage of gonads) indicated peaks in spawning from May until August and a dominant peak in mid-July. Very few gray snapper gonads were collected during the winter months in 1996 and none in 1997 because the majority of gray snapper are landed in July and August (U.S. Dep. Commer.[5]) when they aggregate on offshore reefs to spawn and are probably easier to catch (Starck, 1971; Domeier et al., 1996; Domeier and Colin, 1997). Spawning time has been related to both increasing water temperature and photoperiod for other lutjanids (Arnold et al., 1978; Grimes and Huntsman, 1980).

No obvious temporal differences were observed in reproductive development between regions from adult gonads; however, we determined winter back-calculated fertilization dates for the most southerly part of the sampling region in 1997. In contrast, Domeier et al. (1996) back-calculated spawning dates from June through September using the otoliths from juvenile gray snapper collected from south Florida. Gray snapper larvae have a relatively long pelagic stage of 25 days. The possibility exists that winter-spawned fish were produced from outside the Gulf of Mexico, perhaps from a nearby insular population, and transported from there to settle along the southwestern part of the Florida shelf. The view that winter-spawned fish were Gulf of Mexico expatriates is supported by Grimes's (1987) review of lutjanid reproduction. He found two patterns: 1) continental populations, with extended summer spawning periods; and 2) insular populations, which spawned year-round with pulses in the spring and fall. However, Domeier et al. (1996) suggested after field observations that snapper spawning patterns are species specific, as opposed to habitat dependent. We collected winter-spawned juveniles in only one of the two years of sampling; therefore it is unknown how frequently expatriate settlement events occur and what their importance to gray snapper recruitment might be.

We could not conclusively demonstrate that spawning occurs in association with lunar cycle peaks. Fertilization date hind-cast from otoliths in 1996 were only marginally associated with a lunar cycle and no relationship was evident in 1997 data. Similarly gonad stage data from adult gray snapper did not reveal any lunar pattern. However, the association of spawning with the lunar cycle has been reported for congeneric species, as well as other conspecific populations. Domeier et al. (1996) used a GSI to determine that gray snapper spawning peaked around the time of the new and full moon. Upon examination of adult gonads, Starck (1971) speculated that gray snapper spawned during or near the full moon. The congeneric species *Lutjanus vaigiensis* spawned about the time of the full moon (Randall and Brock, 1960) and *Lutjanus kasmira* spawned during both new and full moons in the laboratory (Suzuki and Hioki, 1979).

Larval duration

Presumed settlement marks were noted in many (60%) of the ageable otoliths, and they were similar in appearance to those observed for several other reef fish species (Brothers and McFarland, 1981; Victor, 1982 and 1986; Sponaugle and Cowen, 1994). Settlement marks are thought to be associated with morphological and ecophysiological changes which occur during the transition from a planktonic to a benthic life stage (Brothers and McFarland, 1981; Victor, 1982; Brothers, 1984). Several lines of evidence suggest that we correctly identified settlement marks. On average, planktonic duration, or length of the presettlement life history phase (i.e. difference between fertilization and settlement dates) was 25 days for both sampling years. Similarly, Koenig and Domeier[6] reported the planktonic

[4] Fitzhugh, G. F. 2000. Unpubl. data. National Marine Fisheries Service, 3500 Delwood Beach Road, Panama City, Florida 32408.

[5] U.S. Department of Commerce. 1998. Fisheries of the United States, 1997. Current fishery statistics no. 9700, 156 p. Statistics Division, Rm. 12340, 1315 East-West Highway, Silver Spring, MD 20910-3282.

[6] Koenig, C. C., and M. L. Domeier. 1993. Unpubl. data. Department of Biological Sciences, The Florida State Univ., Tallahassee, FL 32306-2043.

larval duration to be 24 days (21 d + 3d correction) from otoliths of wild juvenile fish collected off the Florida Keys. Richards and Saksena (1980) recorded settlement for three laboratory-reared gray snapper that were 26, 26, and 36 days old respectively. Thus, gray snapper appear to have a planktonic duration similar to the majority of reef fish (i.e. from 20 to 30 days [Victor, 1991]).

There was no obvious difference in the age at settlement among regions or years. For 1996 and 1997, the temporal distribution of settlement was about the same in the northern and southern parts of the west Florida shelf. In 1997, birth dates and corresponding settlement dates were recorded during the winter months for only the most southern sampling region. Settlement date was marginally associated with the new moon in 1997, possibly reflecting high transport into seagrass meadows at that time. Shenker et al. (1993) found a correlation between onshore transport of settlement-stage Nassau grouper (*Epinephelus striatus*) and the new moon. However, Smith (1995) found no significant association with recruitment of gray snapper through Sebastian Inlet, Florida, and lunar cycle.

Conclusions

This study established that there were differences in the timing of spawning and settlement of gray snapper across the West Florida shelf. Juveniles collected from southwest Florida indicated earlier spawning times than previously reported. Additional year-round sampling of juvenile gray snapper would help to identify the influence of early spawning events on recruitment. Further study of larval transport and genetic markers could aid in the identification of source populations.

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Current velocity and catch efficiency in sampling settlement-stage larvae of coral-reef fishes

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Abstract–Light traps and channel nets are fixed-position devices that involve active and passive sampling, respectively, in the collection of settlement-stage larvae of coral-reef fishes. We compared the abundance, taxonomic composition, and size of such larvae caught by each device deployed simultaneously near two sites that differed substantially in current velocity. Light traps were more selective taxonomically, and the two sampling devices differed significantly in the abundance but not size of taxa caught. Most importantly, light traps and channel nets differed greatly in their catch efficiency between sites: light traps were ineffective in collecting larvae at the relatively high-current site, and channel nets were less efficient in collecting larvae at the low-current site. Use of only one of these sampling methods would clearly result in biased and inaccurate estimates of the spatial variation in larval abundance among locations that differ in current velocity. When selecting a larval sampling device, one must consider not only how well a particular taxon may be represented, but also the environmental conditions under which the device will be deployed.

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With few exceptions, benthic marine organisms exhibit a complex life cycle in which larvae are dispersed pelagically and undergo a planktonic existence before they settle to the sea floor. The vagaries of dispersal by currents and unpredictable mortality of larvae in the plankton contribute to tremendous variation observed in recruitment (here defined broadly as the input of young) to adult populations. For reef fishes, the relative importance of variation in the supply of settlement-stage larvae versus postsettlement density-dependent mortality of recruits to the size and structure of local populations has been debated for some time, with evidence provided for both points of view (Doherty and Williams, 1988; Doherty, 1991; Hixon, 1991; Jones, 1991; Doherty and Fowler, 1994; Hixon and Carr, 1997; Schmitt and Holbrook, 1999). In order to determine the relative contributions of presettlement and postsettlement processes to the population dynamics of reef fishes, knowledge of spatial and temporal variation in the delivery of settlement-stage larvae to local populations is essential.

Various methods have been employed to assess the local abundance of pelagic larvae and juveniles of coral-reef fishes (Choat et al., 1993, and references therein). Two common but relatively recent sampling devices developed to sample settlement-stage reef fish larvae are light traps (Doherty 1987; Thorrold and Milicich 1990; Milicich et al. 1992; Thorrold, 1992; Meekan et al., 1993; Thorrold, 1993; Milicich and Doherty, 1994; Doherty et al., 1996; Sponaugle and Cowen, 1996a, 1996b; Thorrold and Williams, 1996; Doherty and Carleton, 1997; Sponaugle and Cowen, 1997; Leis et al., 1998; Munday et al. 1998; Meekan et al. 2000) and stationary nets, including channel nets (Shenker et al.,1993; Thorrold et al., 1994a, 1994b, 1994c) and crest nets (Dufour and Galzin, 1993; Dufour et al., 1996). Light traps are active sampling devices in that fish are attracted to, swim towards, and enter a transparent or semitransparent trap with a light source. By contrast, channel nets and crest nets passively catch larvae that are carried into them by currents or wave action, respectively. Unlike a previous study that compared light traps with towed nets (Choat et al., 1993), the goal of this study was to compare light traps and fixed-position nets, two commonly used methods for collecting settlement-stage fish larvae near coral reefs.

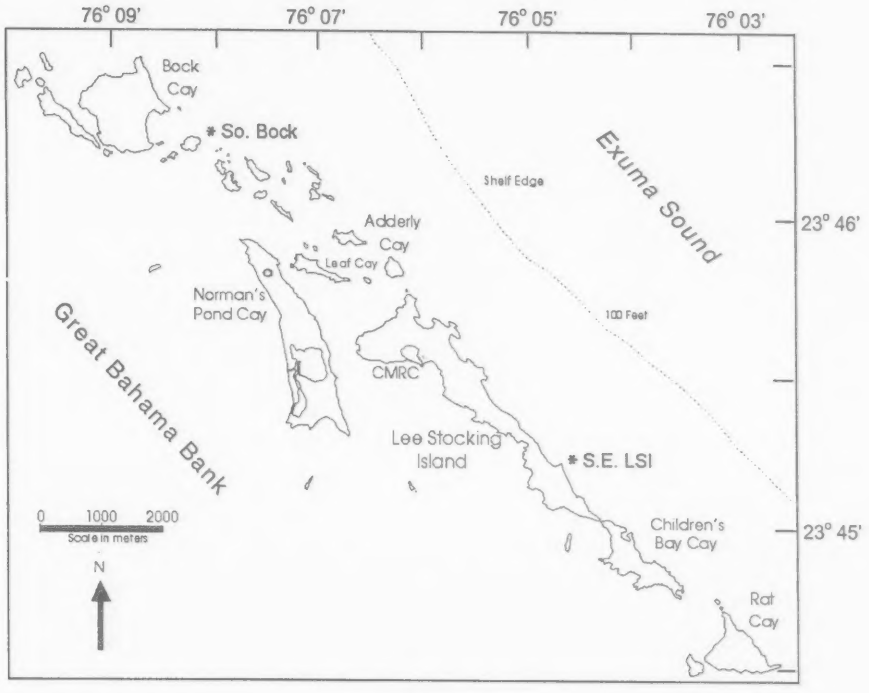

Figure 1

Location of South Bock Cay (So. Bock) and southeast Lee Stocking Island (S.E. LSI) study sites near the Caribbean Marine Research Center (CMRC), Lee Stocking Island, Bahamas.

Light traps and channel nets may not only differ in capture success for any particular species, but in the collection of larvae under varying environmental conditions such as current velocity and turbidity. Species (and the ontogenetic stages of these species) can differ in their sensitivity to light cues (Doherty, 1987; Choat et al., 1993), in swimming ability (Stobutzki and Bellwood, 1994; Leis et al., 1996; Stobutzki and Bellwood, 1997; Wolanski et al., 1997), and in the ability of larvae to interact with current velocity. For example, at relatively high current velocities, settlement-stage larvae that are photopositive but that have limited swimming speeds may not have the ability to respond to a light cue and swim into a light trap as they are carried past the sampling device. Conversely, larvae with strong swimming abilities may be able to avoid capture by channel nets at lower current velocities. Thus the relationship between the sensitivity to light cues and the ability to respond to such cues by larvae (determined by developmental stage, swimming ability, and current velocity) should determine the relative catch efficiency of these sampling devices.

Here we compare and contrast the relative number, taxonomic composition, and size of settlement-stage fish larvae caught in light traps and in channel nets deployed at two reefs that differ substantially in current velocity. Because these devices collect larvae either actively or passively, we examined 1) whether light traps are more selective and catch fewer taxa (families) than channel nets, 2) whether light traps catch larger settlement-stage larvae than channel nets, and 3) with higher current velocity, whether the relative effectiveness of light traps to channel nets decreases, resulting in fewer taxa and a lower abundance of settlement-stage larvae in light traps (with lower current velocity the opposite is true). The relative abundance and taxonomic composition of larvae caught by these two sampling devices, and how they may be modified by current velocity, might result in different interpretations concerning both magnitude and variation in larval supply.

Methods

Study sites

We conducted this study using light traps and channel nets deployed each day, from 30 July through 11 August 1997 at Lee Stocking Island (LSI), Bahamas, bracketing the new moon phase in the lunar cycle when settlement-stage fish larvae are more abundant (Thorrold et al., 1994b). Two fore-reef sites were selected *a priori* for study based upon our impression of marked differences in current velocity: South Bock Cay (So. Bock) northwest of LSI and southeast LSI (S.E. LSI), approximately 7 km south of So. Bock. So. Bock is near a channel between two cays and experiences moderate to strong tidally driven currents, whereas S.E. LSI is far from a channel where there is relatively low current velocity (Fig. 1).

Light traps

We deployed three light traps at each site on each day, from 30 July to 11 August 1997. Each of the three traps at a site was a different modification from two basic designs, with each trap rotated among stations within a site to account for any trap- or location-specific biases. One trap design had a 65-cm diameter polycarbonate top and 1.5-mm nylon mesh enclosing a volume of 200 L, with four clear plastic funnels as fish entrance holes and a fluorescent light powered by nickel-cadmium rechargeable batteries (see Sponaugle and Cowen, 1996b). A second trap design was similar but had an 80-cm diameter wood top instead of a polycarbonate top, a larger volume of 360 L, twice the number of entrance holes, a fluorescent light powered by rechargeable sealed lead-acid batteries, and an automatic timer for turning on the light remotely. The third trap design was composed of a rectangular plexiglas trap (42 cm × 38 cm × 70 cm) with rigid plexiglas panels, a plastic tray, and four entrance slots, constructed to enclose a volume of 110 L based on the design of Munday et al. (1998), but having the same electronics design as that for traps made with polycarbonate tops. All light traps were placed 3–4 m below the sea surface, suspended from moorings with subsurface buoys, and stationed approximately 12–15 m in front of each reef and 50–60 m from each other in a linear array along the offshore edge of the reef. Traps were deployed between 1730 and 1830 h and retrieved the following morning between 0900–1030. All fishes (except for ubiquitous clupeids and atherinids) were collected and placed in vials of 70% or 95% ethanol, identified to family, and later measured with vernier calipers to the nearest 0.1 mm standard length (SL).

Channel nets

We deployed one surface (0–1 m depth) and one subsurface (2–4 m depth) channel net at each site on each day (30 July to 11 August 1997) at a distance of approximately 50 m offshore of the center of the light-trap array. The channel nets were based on the design of Shenker et al. (1993), had a mesh size of 2 mm, and were positioned 30 m apart. The nets were suspended from surface buoys moored to concrete blocks or mooring anchors, allowing them to turn and fish both ebb and flood mixed-semidiurnal tides. The subsurface net mouth opening was 2 m wide × 2 m high. The mouth of each surface net was 2 m wide × 1 m high and was equipped with a General Oceanic Model 2030R2 flow meter and low-speed rotor blade suspended in the mouth opening. Flow-meter readings were recorded from the surface channel net to estimate relative current velocity between the two sites. All nets were equipped with PVC (polyvinylchloride) rods along the length of the netting to prevent entanglement during slack tides, and the codends were constructed to sink and close the end of the net to contain fish larvae during times of very low current velocity. Nets were deployed and retrieved at approximately the same time of day as the light traps. Channel nets were not sampled at dusk to distinguish catches during the day from the following night because previous studies indicated that daytime catches account for a very minor percentage of the total number of fish transported onto the Great Bahama Bank (Shenker et al., 1993; Thorrold et al., 1994c). At the laboratory, samples were rough-sorted to remove debris, fixed with 10% formaldehyde for 24–72 h, and then transferred to 70% isopropyl alcohol for later identification. Fish were measured with vernier calipers to 0.1 mm SL.

Analysis

To compare the number of taxa collected by light traps and channel nets between sites and for both sites combined, we summed the total number of families caught by each sampling device to calculate family richness. We also used the Brillouin index of species diversity (Magurran, 1988) to compare the diversity of families of fish larvae between sampling methods and sites. This index is preferable to the Shannon-Weiner index because samples collected by light traps and channel nets are nonrandom; for example, light traps produce biased samples based on the sensitivity of species to a light cue.

To compare the relative abundance of families caught by light traps and channel nets between sites and for both sites combined, we standardized catches in channel nets to the number of larvae per 1000 m^3, using flow meter readings recorded each day, and we standardized catches from light traps as the number of larvae per day. We could not standarize catches to catch per unit of effort because the length of time that the lights were operational was variable and dependent on the type of light device (see heading "Light traps") and variance in battery life. Moreover, the volume over which light traps attract larvae is difficult to quantify, especially when external factors such as current velocity may largely affect catch rates (Thorrold, 1992; Meekan et al., 2000), and Meekan et al. (2000) suggested that it is useless to convert catch rates into densities.

We used Spearman's rank correlation coefficient (Zar, 1984) to compare the relative abundance of taxa that represented at least 1% of the catch (Choat et al., 1993) for either sampling device. We also used this correlation coefficient to compare the relative abundance of taxa caught by surface and subsurface channel nets between sites for taxa that represented at least 1% of the catch for either net. In order to determine whether there were significant differences in the mean, median, and maximum length of families of fish larvae between light traps and channel nets, we used a Wilcoxon paired-sample test (Zar, 1984) in which differences in length for each family caught by both sampling devices were ranked. Finally, we used a t-test to test for significant differences in current velocity and the proportional abundance of total larvae caught by each sampling device between sites.

Results

Richness, diversity, relative abundance, and individual size

According to our hypotheses in regard to active and passive collection of larvae, both family richness and diversity would differ between light traps and channel nets. A total

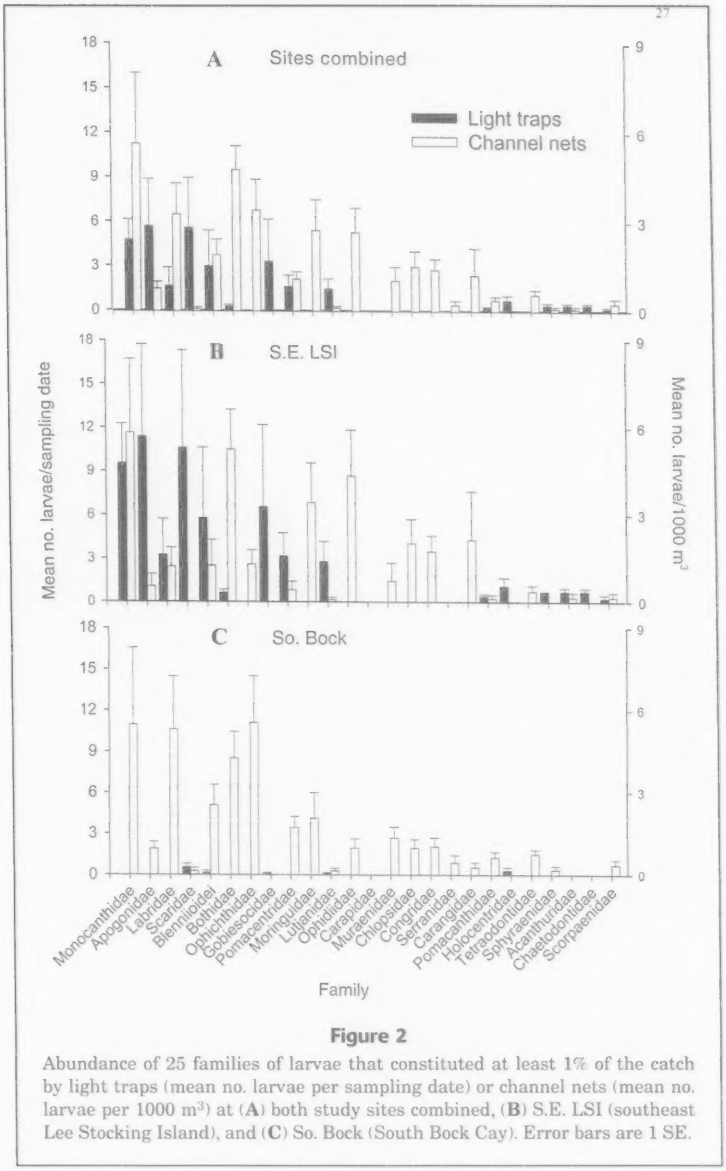

Figure 2

Abundance of 25 families of larvae that constituted at least 1% of the catch by light traps (mean no. larvae per sampling date) or channel nets (mean no. larvae per 1000 m^3) at (**A**) both study sites combined, (**B**) S.E. LSI (southeast Lee Stocking Island), and (**C**) So. Bock (South Bock Cay). Error bars are 1 SE.

of 2111 larvae were collected from light traps (n=849; 78 samples) and channel nets (n=1262; 26 surface and 26 subsurface samples), representing 20 and 33 families, respectively (Table 1), combining blenniids and labrisomids as blennioids, and not including clupeid and atherinid fishes. Synodontids were excluded from further analysis because of the presence of large postsettlement individuals in light traps. For families that constituted at least 1% of the total catch by at least one of these sampling methods, carapids, chaetodontids, gobiesocids, and holocentrids were not caught in channel nets. Conversely, carangids, chlopsids, congrids, muraenids, ophichthids, ophidiids, and tetraodontids were not represented in light-trap samples. Channel nets had higher family richness and diversity at S.E. LSI, So. Bock, and at both sites combined (Table 2) than did light traps.

There was no concordance in the rank order of abundance of families collected by light traps and channel nets at either S.E. LSI (r_s=–0.358, n=25, P>0.05), So. Bock (Spearman's rank correlation coefficient: r_s =–0.120, n=25, P>0.05), or at both sites combined (r_s=–0.162, n=25, P>0.05), including all families that represented at least 1% of the catch of either sampling device (Fig. 2). Similarly, there was no correlation in rank abundance of

Table 1

Total number of fish larvae collected from light traps and channel nets at South Bock Cay and at southeast Lee Stocking Island from 30 July to 11 August 1997. The families Blenniidae and Labrisomidae are combined as Blennioidei. Collections from surface and subsurface channel nets each day have been standardized as no. /1000 m^3. Percentage of total catch of larvae at each site for each family is denoted by (%) for light traps and for channel nets (surface and subsurface nets combined). Asterisks (*) denote families that represented at least 1% of the total catch by light traps or channel nets.

	South Bock Cay					Southeast Lee Stocking Island				
			Channel nets					Channel nets		
Family	Light traps	(%)	Surface	Subsurface	(%)	Light traps	(%)	Surface	Subsurface	(%)
Acanthuridae*						10	(1.2)	0	4.0	(0.5)
Albulidae			9.1	0	(0.9)			0	8.1	(0.9)
Antennariidae			0	1.6	(0.2)			2.4	0	(0.3)
Apogonidae*			14.1	10.7	(2.4)	148	(17.9)	10.6	3.6	(1.6)
Belonidae			1.4	0	(0.1)					
Blenniioidei*	2	(9.5)	24.1	41.8	(6.5)	75	(9.1)	27.4	5.0	(3.7)
Bothidae*			89.3	21.7	(11.0)	8	(1.0)	136.9	0	(15.6)
Callionymidae			0.8	0	(0.1)					
Carangidae*			4.1	3.0	(0.7)			56.0	0	(6.4)
Carapidae*						30	(3.6)			
Chaetodontidae*						9	(1.1)			
Chlopsidae*			24.4	0.9	(2.5)			52.8	0	(6.0)
Congridae*			25.9	0.8	(2.6)			45.4	0	(5.2)
Diodontidae								3.2	0	(0.4)
Exocoetidae			0	0.8	(0.1)					
Gobiesocidae*	1	(4.8)				85	(10.3)			
Gobiidae	2	(9.5)	0	2.4	(0.2)					
Holocentridae*	4	(19.0)				14	(1.7)			
Labridae*			17.8	120.6	(13.7)	42	(4.9)	11.6	20.1	(3.6)
Lutjanidae*	1	(4.8)	1.4	2.3	(0.4)	36	(4.4)	0	2.1	(0.2)
Microdesmidae						1	(0.1)			
Monocanthidae*			118.4	24.0	(14.1)	124	(15.0)	146.1	5.4	(17.3)
Moringuidae*			50.7	2.6	(5.3)			88.8	0	(10.2)
Muraenidae*			33.0	1.6	(3.4)			18.6	0	(2.1)
Ogcocephalidae			4.4	3.4	(0.8)			12.9	0	(1.5)
Ophichthidae*			127.3	16.9	(14.3)			32.4	1.3	(3.8)
Ophidiidae*			18.2	7.1	(2.5)			96.2	16.8	(12.9)
Pomacanthidae*			14.6	1.7	(1.6)	5	(0.6)	3.2	0	(0.4)
Pomacentridae*			35.9	8.9	(4.4)	41	(5.0)	11.0	0	(1.3)
Priacanthidae			1.4	0	(0.1)					
Scaridae*	8	(38.1)	0	3.7	(0.4)	138	(16.7)			
Scorpaenidae*			4.6	4.8	(0.9)	3	(0.4)	4.0	0	(0.5)
Serranidae*			0	11.5	(1.1)					
Sphyraenidae*			4.0	0.8	(0.5)	9	(1.1)			
Syngnathidae			4.5	0	(0.4)	1	(0.1)	18.6	0	(2.1)
Synodontidae	2	(9.5)	1.4	0	(0.1)	48	(5.8)	4.8	0	(0.5)
Tetraodontidae*			17.9	1.7	(1.9)			9.7	0	(1.1)
Unidentified	1	(4.8)	7.3	28.9	(3.6)			12.3	0	(1.4)
Total larvae	21		656.0	324.2		828		804.9	66.4	

Table 2
Richness and diversity of families of fishes caught by light traps and channel nets.

	Sites combined	South Bock Cay	Southeast Lee Stocking Island
Richness (no. families)			
Light traps	19	6	18
Channel nets	32	30	23
Diversity (Brillouin index)			
Light traps	2.845	1.179	2.832
Channel nets	3.183	3.199	3.027

subsurface and surface channel nets, including only those families that represented 1% of the catch of either net for S.E. LSI (r_s=0.227, n=16, P>0.05; Fig. 3A) or for So. Bock (r_s=0.088, n=16, P>0.05; Fig. 3B). In addition, the sizes of larvae (Table 3) caught by light traps and channel nets (but excluding families with <3 individuals collected per sampling device [acanthurids, gobiids, and syngnathids]) did not differ in the mean (sign test: n=11, P>0.05), median (n=11, P>0.05), or maximum (n=11, P>0.05) length between sampling devices. For five families that differed in length between sites and that were represented by at least three individuals (Table 3), channel nets caught significantly larger larvae at S.E. LSI than at So. Bock in mean (n=5, P=0.03) and median (n=5, P=0.03) length, but not in maximum length (n=5, P>0.05).

Current velocity and catch efficiency

Over a 10-d period in which flow-meter readings were taken simultaneously at both sites, mean daily current velocity was three-times higher at So. Bock than at S.E. LSI (t-test: t=–7.92, df=18, P=0.0001; Fig 4A). Light traps deployed at So. Bock caught on average only 3.1% of the total number of fish collected by light traps at both sites, whereas the channel nets positioned at S.E. LSI caught an average of 43.8% of the total catch for nets positioned at both sites (Fig. 4B). The mean proportional abundance of all larvae caught by light traps was significantly lower at So. Bock than at S.E. LSI (t =–50.3, df=24, P<0.0001) but there was no significant difference in proportional catch for channel nets (t=1.36, df=24, P=0.19). The difference in catch efficiency for each sampling device was also indicated by the opposite trends of abundance of taxa (apogonids, blennioids, labrids, pomacentrids, but not monocanthids) caught in at least nominally greater numbers by light traps at the low-current site (S.E. LSI) compared with the greater catch of these same taxa by channel nets at the high-current site (So. Bock). In addition, and consistent with our hypotheses concerning current velocity, light traps had higher family richness and diversity at S.E. LSI than at So. Bock, whereas the opposite was true for channel nets (Table 2).

Discussion

Differential representation of taxa between sampling methods

Light traps and channel nets differed in the taxonomic composition and the relative abundance of their catch. Expectedly, channel nets had appreciably higher family richness and diversity than did light traps, and this is consistent with our hypothesis that light traps are more selective (also see Choat et al., 1993) because not all larvae exhibit a photopositive response. One of the main differences in the relative abundance of larvae between sampling devices in the central Bahamas is that channel nets collect a large proportion of labrids and leptocephalus larvae (Shenker et al., 1993; Thorrold et al., 1994a, 1994b, 1994c; Mojica et al., 1995; this study) but light traps do not (this study). Depth-dependent distributions of larvae are also likely to contribute to differences in the relative abundance of taxa because light traps catch larvae from an unknown depth range (over which larvae are attracted to the light) whereas surface and subsurface channel nets operate at discrete depths of 0–1 m and 2–4 m, respectively. Moreover, not only can surface and subsurface channel nets differ in their catch (Fig. 3), the relative abundance of particular taxa between surface and subsurface nets can switch over time (Thorrold et al., 1994c).

The similar sizes of larvae from families caught by both light traps and channel nets are somewhat inconsistent with the findings by Choat et al. (1993), who found that larvae caught by light traps were larger than those caught by towed nets and seines. They attributed this differerence in size to a stronger photopositive response by larger pelagic larvae. The smaller size of larvae that they caught in towed nets and seines may also indicate that larger larvae may better sense the presence of these nets and avoid capture. Channel nets may decrease net avoidance by larvae because their stationary position may lessen water disturbance and hence detection of the net by incoming larvae, or possibly because other larval behaviors are exhibited.

Differential representation of taxa between sites

The greatest difference between light traps and channel nets was in their relative catch between sites. Light traps were ineffective in collecting larvae at So. Bock, whereas channel nets collected a lower but not significantly different proportion of larvae at S.E. LSI. This result cannot be explained simply by differences in the abundance of taxa between sites; the same pattern was observed for taxa sufficiently represented by both sampling devices (apogonids, blennioids, labrids, pomacentrids). These sites did differ substantially in mean current velocity, with average flow rates at So. Bock three times higher than at S.E. LSI. Shenker et al. (1993) observed that larvae collected by channel nets were significantly more abundant at a sampling station that also had greater current velocity, and this finding is consistent with our results. Similarly, Thorrold (1992) observed that light traps that were allowed to drift with water masses collected signifi-

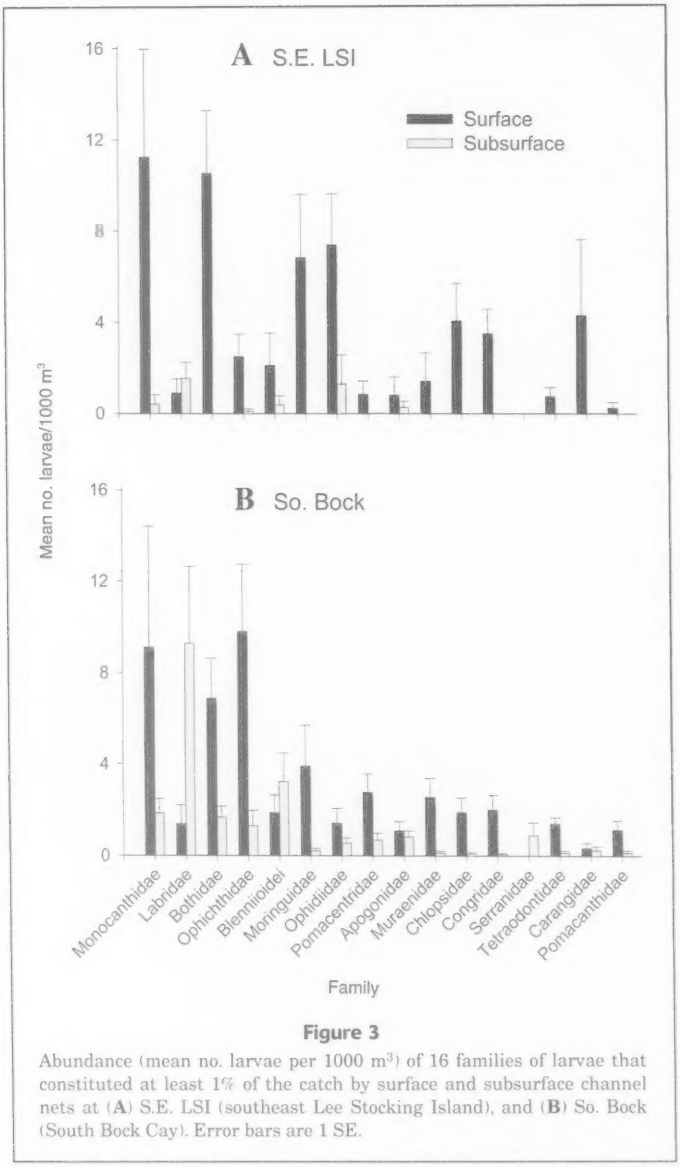

Figure 3

Abundance (mean no. larvae per 1000 m^3) of 16 families of larvae that constituted at least 1% of the catch by surface and subsurface channel nets at (**A**) S.E. LSI (southeast Lee Stocking Island), and (**B**) So. Bock (South Bock Cay). Error bars are 1 SE.

cantly more fish larvae than light traps anchored to the sea floor, apparently independent of taxa. Thorrold noted that this pattern was unexpected because more water (and presumably more larvae) should pass by anchored traps, and he suggested that the ability of larvae to swim to and enter anchored traps may be difficult under high-current conditions.

Although we conclude that between-site differences in relative catch by light traps and channel nets in our study were related to current velocity, the relationship between catch and average current velocity was not linear. The proportional abundance of larvae caught in light traps was over 31 times higher at S.E. LSI than at So. Bock, whereas the larval catch in channel nets was only 1.3 times higher at So. Bock than at S.E. LSI. The nonlinear relationship between current velocity and larval abundance may represent a threshold response in which the efficiency of light traps and channel nets may change with different current velocities. The mechanisms causing such relationships might be that fish larvae are able to orient to and swim into light traps more easily under lower current velocities, whereas fish larvae might more easily detect and avoid channel nets because of greater hydrodynamic disturbances in front of nets during higher current velocities.

Table 3

Mean (±1 SE), median, and range in size of larvae (mm standard length) collected in light traps and channel nets at South Bock Cay and at southeast Lee Stocking Island from 30 July to 11 August 1997. The families Blenniidae and Labrisomidae are combined as Blennioidei.

	South Bock Cay				Southeast Lee Stocking Island			
Family	Mean (SE)	Median	Range	*n*	Mean (SE)	Median	Range	*n*
Light traps								
Acanthuridae					25.3 (0.31)	25.2	(24.2–26.9)	9
Apogonidae					9.1 (0.12)	8.6	(6.6–14.2)	150
Blennioidei	12.6 (0.20)	12.6	(12.4–12.8)	2	11.8 (0.18)	11.6	(7.8–18.7)	83
Bothidae					13.7 (0.45)	13.5	(12.0–15.0)	7
Gobiidae	8.8 (0.10)	8.8	(8.7–8.9)	2				
Labridae					9.3 (0.29)	8.6	(6.9–12.3)	32
Lutjanidae	11.7	11.7	(11.7–11.7)	1	15.0 (0.39)	14.3	(12.6–20.8)	29
Monocanthidae					11.9 (0.19)	11.4	(7.4–21.4)	128
Pomacanthidae	13.9	13.9	(13.9–13.9)	1	9.0 (0.24)	9.1	(8.3–9.4)	4
Pomacentridae					10.9 (0.21)	10.8	(8.7–13.7)	40
Scaridae	9.1 (0.24)	8.9	(8.7–10.3)	6	8.6 (0.08)	8.7	(5.9–10.8)	120
Scorpaenidae					6.8 (0.20)	6.8	(6.4–7.1)	3
Sphyraenidae					18.0 (0.90)	18.4	(13.0–21.5)	9
Syngnathidae					40.5	40.5	(40.5–40.5)	
Channel nets								
Acanthuridae					24.7	24.7	(24.7–24.7)	1
Apogonidae	10.2 (0.24)	9.8	(8.9–14.2)	26	9.8 (0.43)	9.8	(9.0–10.5)	3
Blennioidei	12.7 (0.12)	12.7	(10.8–17.8)	65	13.6 (0.76)	12.8	(11.6–18.1)	8
Bothidae	14.8 (0.14)	14.8	(7.0–17.8)	103	16.0 (0.77)	15.1	(12.0–36.2)	29
Gobiidae	13.5 (0.24)	13.6	(13.0–13.8)	3				
Labridae	11.4 (0.06)	11.4	(9.5–13.6)	154	13.7 (1.3)	12.4	(10.9–28.7)	13
Lutjanidae	13.6 (0.38)	13.7	(12.0–14.7)	6	11.8	11.8	(11.8–11.8)	1
Monocanthidae	12.2 (0.24)	12.0	(5.2–51.3)	204	12.8 (0.29)	13.0	(7.7–18.6)	45
Pomacanthidae	8.9 (0.14)	9.0	(7.5–9.4)	12	9.2	9.2	(9.2–9.2)	1
Pomacentridae	10.2 (0.20)	9.8	(8.8–13.9)	32	12.6 (0.95)	11.8	(11.5–14.5)	3
Scaridae	9.0 (0.13)	9.0	(8.6–9.2)	4				
Scorpaenidae	8.0 (0.35)	8.1	(6.7–9.6)	9	8.1	8.1	(8.1–8.1)	1
Sphyraenidae	23.9	23.9	(23.9–23.9)	1	18.6 (3.9)	19.9	(11.3–24.6)	3
Syngnathidae	32.9 (16.9)	25.7	(7.8–65.1)	3	35.0 (1.8)	35.0	(33.2–36.8)	2

Indeed, there may be important consequences in sampling reef fish larvae among multiple sites that vary in current velocity. Current-dependent catch efficiency could confound estimates of spatial variation in larval abundance if those sites vary substantially in current velocity. For example, deploying light traps to sample larval abundance at several locations may result in higher abundances at sites with low current. This result could indicate actual larval distributions, such as accumulation of larvae on the leeward side of an island, or it could simply reflect current-dependent catch efficiency. In the latter case, estimates of larval distribution and subsequent interpretations of such distributions (e.g. larval retention) would be flawed.

As with all sampling devices, light traps and channel nets have both advantages and disadvantages for estimating larval abundance. Light traps may collect a larger proportion of settlement-stage larvae for those fishes that exhibit a photopositive response, but they catch fewer taxa and sample an unknown volume of water (Choat et al., 1993) in relation to channel nets. Our results indicate an important factor in selecting an appropriate device for estimating larval supply—namely, the hydrodynamic conditions under which the device will be deployed. Use of one sampling device, either light traps or channel nets, would have resulted in biased and potentially inaccurate relative estimates of larval abundance between So. Bock and S.E. LSI. In more recent studies, several methods have been used to estimate the abundance of as many larval fishes as possible (e.g. Leis et al., 1998), and in a comparison of light traps and towed nets in sampling freshwater fishes, Gregory and Powles (1988) concluded that both sampling devices should be used to avoid bias in the collection of larvae.

The use of both light traps and channel nets simultaneously can provide less biased estimates of spatial variation in taxonomic composition and larval supply of coral-reef fishes among sites that vary in current velocity. This com-

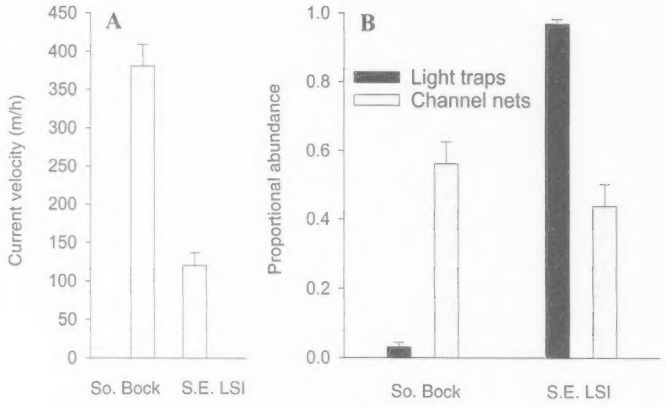

Figure 4

(**A**) Mean current velocity averaged over 24 h (m/h), and (**B**) mean daily proportional abundance of larvae caught by light traps and channel nets at So. Bock (South Bock Cay) and at S.E. LSI (southeast Lee Stocking Island). Error bars are 1 SE.

bination is problematic, however, because there is no "common currency" between light traps and channel nets. The volume of water sampled by light traps is unknown, and capture rates of larvae are very low (Meekan et al., 2000), so that the catches of light traps and channel nets cannot be easily standardized. The value of these and other larval sampling devices is that they provide a measure of temporal and spatial variation in relation to larval supply. However, the nonlinear relationship between current velocity and larval abundances observed in our study could compromise such estimates and further complicate standardization among sampling devices. Additional research is necessary to account for method-dependent differences in larval abundance among sites that differ in hydrodynamic or other environmental conditions.

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Intermingling and seasonal migrations of Greenland halibut (*Reinhardtius hippoglossoides*) populations determined from tagging studies

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Abstract—A total of 7244 Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) were tagged in Greenland waters between 1986 and 1998 to increase information on stock delineations, to clarify migration routes, and to describe the seasonal movements of fjord populations. At present 517 recaptured Greenland halibut have been recorded. For Greenland halibut released in Davis Strait, Baffin Bay, and the fjords of southwestern and eastern Greenland, a substantial portion of recovered fish demonstrated migratory behavior, up to 2500 km, primarily to Denmark Strait between Greenland and Iceland. The recaptured fish provided evidence of intermingling between the population in Denmark Strait and the populations in Davis Strait and the southwest Greenland fjords. These observations support those of other studies that indicate that Greenland halibut inhabiting Davis Strait and the fjords of southwestern and eastern Greenland originate in the spawning grounds west of Iceland. The high mobility of offshore Greenland halibut within Baffin Bay and Davis Strait suggests that Greenland halibut migrate extensively between feeding and spawning areas. Greenland halibut in the fjords of northwestern Greenland appear to be resident in behavior and do not intermingle with offshore or more southerly inshore populations. A seasonal pattern in the recovery of these fish indicates that Greenland halibut aggregate in the inner part of fjords during the second half of the year (when inshore waters are not covered with ice).

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Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), are widely distributed in the Northwest Atlantic. Their range covers a geographical area from Smith Sound, between Greenland and Canada, southward throughout Baffin Bay and Davis Strait to the northeastern coast of the United States and eastward along eastern Greenland to Iceland (Smidt, 1969; Bowering and Brodie, 1995). The spawning grounds of Greenland halibut are believed to be located southwest of Iceland (Sigurdsson[1]) and cover an extended area from Davis Strait, south of 67°N (Jensen, 1935; Smidt, 1969) to south of Flemish Pass off Newfoundland (Junquera and Zamarro, 1994) between 800 and 2000 m depths. The Greenland halibut populations off the eastern coast of Canada, in Davis Strait, in the fjords of western Greenland, in the Denmark Strait, and in Icelandic waters are believed to be recruited from these spawning grounds (Templeman, 1973; Sigurdsson[1]). A number of scientists have examined interactions among different local populations of Greenland halibut in the Northwest Atlantic. They have considered and, in some cases, attempted to quantify meristic characteristics (Templeman, 1970; Misra and Bowering, 1984; Riget et al., 1992; Rasmussen et al., 1999), genetic variability (Fairbairn, 1981; Riget et al., 1992; Vis et al., 1997), the occurrence of parasites as natural tags (Khan et al., 1982; Boje et al., 1997), and tagging data (Smidt, 1969; Bowering, 1984; Riget and Boje, 1989; Boje[2]). The results of these investigations suggest that the entire Greenland halibut population between Greenland and Canada must be considered a single stock unit. There is some evidence that the populations between Greenland and Iceland originate from a spawning stock situated along the continental slopes west of Iceland. A number of Greenland halibut populations seem to maintain a degree of isolation without any prespawning migration to their original spawning areas; this is characteristic of the Greenland halibut population in the Gulf of St. Lawrence (Khan et al., 1982) as well as for populations in the fjords of northwestern Greenland (Riget and Boje, 1989). Spawning has been observed in the Gulf of St. Lawrence (Bowering, 1980), but only a few ripe females have been sighted in the fjords of western Greenland (Riget and Boje, 1989).

Previous tagging experiments in the fjords of western Greenland (Smidt, 1969; Riget and Boje, 1989; Boje[2]) suggest that Greenland halibut stocks in the southernmost fjords may be recruited from Icelandic spawning grounds. The Irminger Current and the East Greenland Polar Current carry eggs and larvae from these spawning

[1] Sigurdsson, A. 1979. The Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)) at Iceland. Hafrannsóknir, 16, Marine Research Institute, Reykjavik, Iceland.

[2] Boje, J. 1993. Migrations of Greenland halibut in the Northwest Atlantic from tagging experiments in West Greenland 1986–89. ICES (International Council for the Exploration of the Sea) C. M. Doc. 1993/G:65, 14 p. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

grounds to eastern Greenland and probably as far as southwestern Greenland (Sigurdsson[1]; Boje[3]). In 1959, Smidt (1969) observed the recapture west of Iceland of Greenland halibut that had been tagged in Licthenau Fjord in southwestern Greenland in 1954. Riget and Boje (1989) noted the recapture west of Iceland in 1980 of Greenland halibut that had been tagged in Godthaab Fjord in 1964.

In the present study, tagging experiments in the fjords of eastern and western Greenland from 1986 to 1998 are evaluated to determine the stock discreteness of Greenland halibut populations in the Northwest Atlantic and to describe seasonal migrations of Greenland halibut within inshore areas.

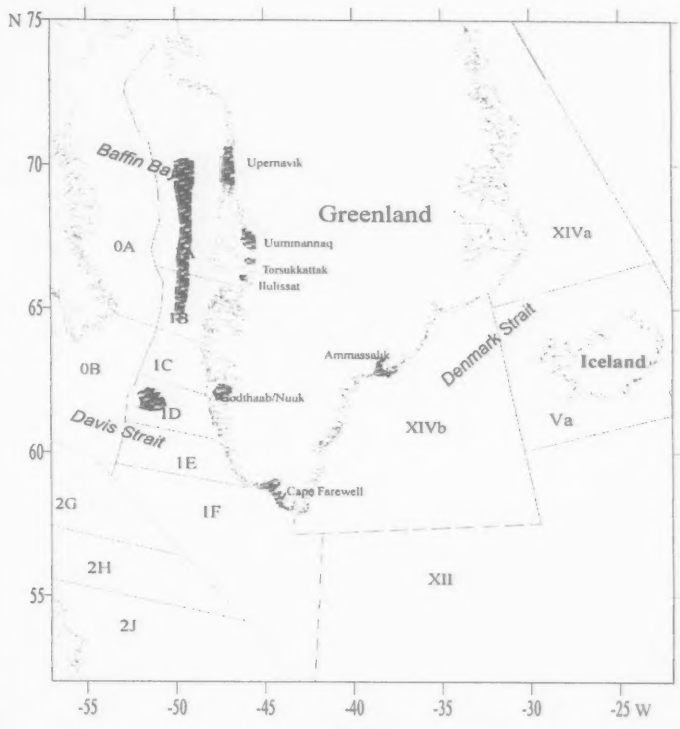

Figure 1

Map of release sites (shaded areas). NAFO (Northwest Atlantic Fisheries Organization) (0–2) and ICES (International Council for the Exploration of the Sea) (V–XIV) divisions are indicated.

Materials and methods

Greenland halibut from four areas around Greenland were tagged between 1986 and 1998. The tagging was carried out in the fjords of eastern Greenland at Ammassalik in September 1990, in the fjords of southwestern Greenland from Cape Farewell to Godthaab Fjord in January 1987–88, in the fjords of northwestern Greenland from Disko Bay to Upernavik during July–August 1986–98, and off western Greenland from Davis Strait to Baffin Bay during May–August 1991–93 (Table 1, Fig. 1). Samples were collected with longlines (Mustad Autoline Systems) from research vessels fishing at depths between 400 and 900 m—a range that is standard for the commercial fishery (Boje[4]). Fishing time for each set was approximately six hours.

A landing net was placed under each fish from the time it left the water until the fish was landed onboard the ship to avoid damage from the hook (i.e. the gravitational drag of the hook while the specimen was removed from the water). The hook was removed with care and only fish hooked in the mouth region were selected for tagging because these injuries were generally not fatal. Condition of the fish was judged visually, mainly by examining the color of the gills and by assessing internal hooking injuries. Length of the fish was measured to the nearest full centimeter (total length) and fish larger than 35 cm were selected to increase the possibility of immediate recapture in the fishery. Each fish was tagged in the musculature with a yellow T-bar tag (Floy T-bar anchor tags, FD-68B yellow) just below the dorsal fin ray near the head. Immediately after having been tagged, the fish was released.

For an evaluation of migratory routes, the numbers of recaptured fish were adjusted for fishing activities (annual landings) in recapture area (i.e. NAFO/ICES division) for the year of recapture and these numbers were expressed as the number of halibut per 100 metric tons of annual landings in the recapture division. Landing statistics were obtained from Greenland Statistical Office, NAFO Statistical Bulletin 1986–93, NAFO STATLANT 21A data and ICES Cooperative Research Reports of the ACFM 1986–98.

To analyze seasonal movements among "resident" Greenland halibut (i.e. fish caught less than 100 km from the release site) of northwestern Greenland, the fjords were stratified into five rectangles of equal area, and positioned in an east–west direction. A random-walk model (Skellam, 1951) was applied to the distribution of all releases (n=4319) pooled for the entire period, 1986–98, for all five areas, assuming equal probability that the fish would migrate either east or west or remain in the area (P=0.33). The model operated on a time unit of three months, thereby allowing each fish to move from only one rectangle to the next rectangle within a quarter of a year.

[3] Boje, J. 1997. Larval growth and spawning of Greenland halibut in West Greenland waters and the possible influences by hydrographic conditions. ICES (International Council for the Exploration of the Sea) international symposium on "Recruitment dynamics of exploited marine populations: physical-biological interactions," Baltimore 22–24 Sept. 1997. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

[4] Boje, J. 1989. The fishery for Greenland halibut in Subarea 1. NAFO (Northwest Atlantic Fisheries Organization) SCR Doc. 89/27, ser. N1603, 8 p.

Table 1

Summary of numbers of tagged and recaptured Greenland halibut since 1986, comprising 517 recaptured halibut of a total of 7244 tagged fish. All fish were captured by means of longlines.

Data on tagging experiments							Information on recaptured halibut											
							Calendar years after release											
Site	Year	Month	Location	NAFO/ ICES area	Length range (cm)	Number released	0	1	2	3	4	5	6	7	8	Un-known	Total number	% of released
East Greenland fjords	1990	September	Ammassalik	XIVb	40–74	183		6	3	3	9	1		1			23	12.6
Southwest Greenland fjords	1988	January	Cape Farewell	1F	35–91	120	4	1	2	1			1				9	7.5
	1987	January	Godthaab Fjord	1D	34–110	839	14	20	9	1		1		1			46	5.5
Northwest Greenland fjords	1986	August	Ilulissat	1A	33–95	43		1	1		1						3	7.0
	1987	August	Ilulissat	1A	30–90	154	1	2	4	5	2			1			15	9.7
	1993	August	Ilulissat	1A	26–96	34											0	
	1994	August	Ilulissat	1A	34–68	71	4	2	1								7	9.9
	1986	August	Torsukkattak	1A	31–85	272	1	6	5		3	2			1		18	6.6
	1987	August	Torsukkattak	1A	38–100	384	8	21	8	10	2					3	52	13.5
	1993	August	Torsukkattak	1A	48–82	88	7	10	7								24	27.3
	1994	July	Torsukkattak	1A	36–92	144	4	14			1						19	13.2
	1996	August	Torsukkattak	1A	49–76	31	1	1									2	6.1
	1997	July	Torsukkattak	1A	44–93	264	3	15									18	6.8
	1987	August	Uummannaq	1A	36–98	244	2	7	3	8	3	3		1			27	11.1
	1993	August	Uummannaq	1A	39–87	136	3	12	6	1	2						24	17.6
	1994	August	Uummannaq	1A	42–84	49	1	2	1	1							5	10.2
	1995	August	Uummannaq	1A	41–83	363	4	25	16	4							49	14.0
	1996	August	Uummannaq	1A	39–79	574	2	21	10								33	5.7
	1998	July	Uummannaq	1A	40–80	454	13										13	2.9
	1989	August	Upernavik	1A	35–107	634	2	26	15	14	9	8	2	1			77	12.1
	1990	August	Upernavik	1A	39–106	41											0	
	1994	July	Upernavik	1A	46–92	162	4	12	5								21	13.0
	1995	July	Upernavik	1A	38–88	177	2	6	2	1							11	6.2
West Greenland offshore	1991	August	Davis Strait	1D	42–109	682	5		1	2	1			1			10	1.5
	1992	May	Davis Strait	1D	36–101	385	3	1	2			1					7	1.8
	1993	August	Baffin Bay	1A	43–92	716		1			1	2					4	0.6
Totals					26–110	7244	88	212	101	51	34	18	3	6	1	3	517	7.1

The model run covered a total of eight years, which was the maximum time recorded for time at liberty of tagged Greenland halibut at sea. The random walk distribution was compared with the true recapture distribution by means of a chi-square test. The true recapture distribution was corrected for fishing effort by using the frequency of recaptured halibut per unit landing in a statistical square (smallest statistical unit to assign landings), where landings were monthly averages for the period 1993–97. By pooling landings monthly for this 5-year period there were no zero values in the data set. Effort data were not available for the inshore fishery; therefore landings data were used instead. Previously landings data for these inshore areas were found to correlate well with fishing effort (Anonymous, 1998).

Migration distances are given in kilometers (1 km=0.540 nautical mile). For all analyses, SAS statistical (SAS, 1988) and Statistica (StatSoft, Inc., 2000) software were used.

Results

A total of 7244 Greenland halibut were tagged from 1986 to 1998. By the end of 1998, 517 recaptured Greenland halibut (7.1% of halibut released during the entire period) were recovered (Table 1). The majority of recaptured fish were reported within two years after tagging, but some were reported as late as eight years after tagging. In general, Greenland halibut tagged in the fjords of northwestern Greenland (Ilulissat, Torsukkattak, Uummannaq, and Upernavik) tended to remain resident, whereas some Greenland halibut from the three other tagging sites (East Greenland fjords, Southwest Greenland fjords, and West Greenland offshore) displayed migratory behavior.

Prevailing migratory patterns

An overview of the numbers of recaptured Greenland halibut (adjusted for fishing activity for each release site versus recapture area) is presented in Table 2. Most recaptured Greenland halibut were found at their release locality (especially at Ammassalik in East Greenland, in the fjords of Cape Farewell, in Godthaab Fjord, Uummannaq, and Upernavik in West Greenland), and 99% of the recaptured halibut were taken within the release area. For releases in the two neighboring fjords in northwestern Greenland, Ilulissat, and Torsukkattak, 10–14% of recaptured Greenland halibut showed intermingling between the two fjords. Limited intermingling was also noted between Ilulissat and Uummannaq (<1–3%). Of the 21 recaptured Greenland halibut from Davis Strait and Baffin Bay, 96% and 77%, respectively, were caught in the release area (values adjusted for fishing effort). Of 23 recaptured Greenland halibut in Ammassalik in East Greenland, the vast majority (99%) were recaptured near the tagging site; whereas single specimens (less than 1%) were recaptured in Denmark Strait and north of the Faroe Islands. Greenland halibut recovered from releases in the fjords of southwestern Greenland (Cape Farewell and Godthaab Fjord,) were mostly recaptured at the release site (99%), whereas the remaining were captured in Denmark Strait, except for a single specimen captured off Newfoundland. The majority of released halibut from the most comprehensive tagging effort in the fjords of northwestern Greenland were recaptured at their tagging site (approximately 90%). This observed fidelity to tagging site was most pronounced in the northern areas of the fjord systems at Uummannaq and Upernavik. No released fish from the fjords of northwestern Greenland were recaptured outside the area. Of the halibut released in the offshore areas of western Greenland, i.e. Davis Strait and Baffin Bay, most were recovered at their release sites, but a few specimens were also recovered as far as Denmark Strait and Newfoundland. Although only four Greenland halibut were recaptured from Baffin Bay, two of them were captured in the fjord of northwestern Greenland (Torsukkattak). Adjusted for fishing effort, they accounted for 17% of recaptured Greenland halibut from Baffin Bay.

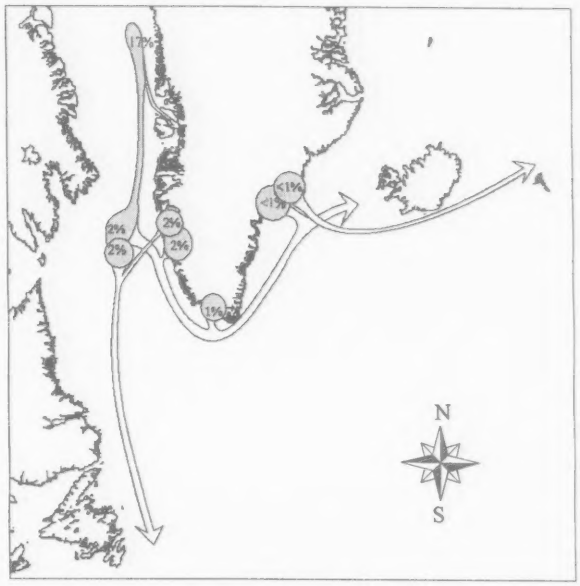

Figure 2

Migration pattern for long-distance migrants only. Numbers indicate percentage of recaptured fish from different tagging sites in Greenland that were caught at fishing grounds shown by the arrows (northwestern Greenland Fjord Torsukkattak, off Newfoundland, west of Iceland, and north of the Faroe Islands).

Long-distance migrants

Twenty-three specimens were recovered at substantial distances from their release sites (Fig. 2). Greenland halibut tagged in Godthaab Fjord and recaptured in Denmark Strait (6 specimens) migrated an average of approximately

Table 2

Summary of data for recaptured Greenland halibut by release location and recapture area (upper numbers represent numbers adjusted for fishing effort, numbers in parentheses are percentages).

Release location	Recapture area												Total recaptured halibut (not adjusted)
	Faroe Islands	Denmark Strait	Ammassalik	Cape Farewell	Godthaab Fjord	Newfoundland	Davis Strait	Ilulissat	Torsukkattak	Upernavik	Uummannaq		
Ammassalik	2 (<1)	2 (<1)	23000 (99)										23
Cape Farewell		1 (<1)		569 (99)									9
Godthaab Fjord		1 (<1)			1459 (99)	1 (<1)							46
Davis Strait		1 (2)				1 (2)	34 (96)						17
Baffin Bay		1 (5)					17 (77)		4 (17)				4
Ilulissat								98 (83)	16 (14)		3 (3)		26
Torsukkattak								67 (10)	614 (90)				113
Uummannaq								3 (<1)			313 (99)		153
Upernavik									3 (<1)	523 (99)	4 (<1)		108
Total recaptures (not adjusted)	1	17	16	7	39	3	14	42	100	105	155		499[1]

[1] Only 499 fish of 517 fish total recaptured had reliable information on recapture position.

1100 km: whereas fish released in Godthaab Fjord and Davis Strait and recaptured off Newfoundland (1 and 2, respectively) migrated an average of 1800 km. A single fish recaptured north of the Faroe Islands was released at Ammassalik in eastern Greenland. All recaptured Greenland halibut in Denmark Strait had been released at inshore areas of eastern and southern Greenland or from offshore areas of western Greenland. From the latter area, one fish tagged in Baffin Bay had thus migrated about 2500 km. Recaptured Greenland halibut off Newfoundland were tagged in Davis Strait and Godthaab Fjord. Two fish released from Baffin Bay were recaptured in the northern fjord of Disko Bay (Torsukkattak).

A cumulative distribution of estimated migration distance for each main release site (Fig. 3) revealed that Greenland halibut from the offshore area of western Greenland were the more frequent long-distance migrants, and only about 50% were resident. About 70% of recaptured Greenland halibut from East Greenland fjords migrated 400 km or less. Approximately 80% of Greenland halibut from the fjords of southwestern Greenland were resident, whereas the remaining 20% undertook migrations of 1000–1200 km. Nearly all Greenland halibut in the northwestern fjords were resident and migrated less than 100 km.

Inshore seasonal migration

Recapture data from the fjords of northwestern Greenland were examined to determine whether recapture location varied seasonally, i.e. whether seasonal migrations occurred. The inshore fishery is carried out in all seasons mainly with longlines. Catches tend to peak during the warmer period in July–August, when water is free from ice in the inner part of the fjords, but substantial numbers are also caught from January to June, when waters are covered by ice, in a fishery distributed throughout

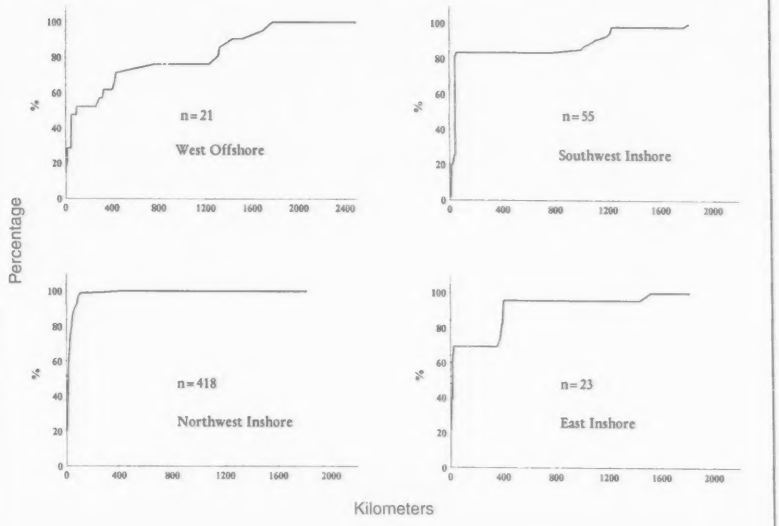

Figure 3

Cumulative distribution of distance (km) migrated by released Greenland halibut from four main areas. *n* = number of recaptured fish.

the fjord (Simonsen and Boje[5]). The catch-adjusted recapture data were categorized by stratifying the fjords into five rectangles of equal area, ranging from the mouth of the fjord to the inner part of the fjord. A chi-square test on the real recapture distribution compared with a random-walk distribution based on pooled release data, proved significant ($P<0.0001$), indicating that Greenland halibut do not migrate randomly in the fjord system, but tend to aggregate at specific localities at certain times of the year. Pooling the data by ice-cover period (1st and 2nd quarters) and open-water period (3rd and 4th quarters) and weighing the distribution within each quarter equally also resulted in significantly different distributions between the real data and the random-walk data. The real pooled data, shown by quarters (Fig. 4), demonstrated that Greenland halibut display a dispersed distribution during the ice-cover period (1st and 2nd quarters) but concentrate in the inner parts of the fjords during the open-water period (3rd and 4th quarters). The steep gradient from the 4th to the 1st quarter may be due to the fishing practices of the commercial fisheries, which are virtually dormant between November and February. Thus fish recaptured from the fishery for the two quarters mainly represent only the months of October and March, respectively .

[5] Simonsen, C. S., and J. Boje. 2000. An assessment of the Greenland halibut stock component in NAFO Division 1A inshore. NAFO (Northwest Atlantic Fisheries Organziaton) SCR Doc. 00/47, ser. N4278, 37 p. NAFO Secretariat, 2 Morris Drive, P. O. Box 638, P. O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

Discussion

Sampling by hook-and-line gear does not reflect the true abundance of Greenland halibut in prespawning and spawning conditions. But, because the majority of the tagging took place outside the spawning period (winter and early spring), the sampling gear should not have biased any recovery patterns. Tagging in the southwest Greenland fjords took place in January, but the recovery pattern for those areas was confirmed by tagging data from other seasons of the year (Riget and Boje, 1989). Therefore, I assumed that any tagged specimens represent feeding fish, not spawning groups of the population.

Although Greenland halibut demonstrated long-distance displacements of about 2500 km in a two-year period, most recoveries indicated rather limited movement. The majority of tagged and recaptured Greenland halibut in this study support the current understanding of stock relationships among Greenland halibut populations (Bowering and Brodie, 1995; Boje et al., 1997; Vis et al., 1997). However, several cases of single recoveries suggest links between halibut populations not considered before. One fish recorded off Newfoundland had been released in Godthaab Fjord two years earlier, yet currently it is believed that Greenland halibut from Godthaab Fjord and other fjords of southwestern Greenland originate from the Icelandic spawning stock (Smidt, 1969; Riget et al., 1989; Boje, 1993). Released Greenland halibut from Baffin Bay yielded single recoveries in the northwestern Greenland fjord of Torsukkattak and in Denmark Strait. The latter is a migration distance of about 2500 km. Also, one Greenland halibut released in eastern Greenland at

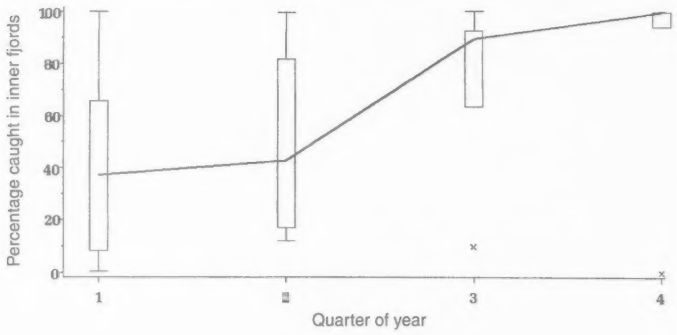

Figure 4

Box plot of proportion of Greenland halibut recaptured in the inner part of fjords in relation to those recaptured in the entire fjord system shown by season, according to pooled tagging-recapture data. Median values are joined by a solid line, boxes represent 25th and 5th percentiles, and horizontal "whiskers" represent 95% confidence limits. Outliers are indicated by crosses.

Ammassalik was recaptured north of the Faroe Islands four years after release, which indicates a link between the Greenland halibut populations in the Northwest Atlantic and those in the Northeast Atlantic and suggests some intermingling of halibut populations in the Atlantic Ocean. Studies on genetic differentiation have shown that Greenland halibut in the North Atlantic are genetically homogenous, indicating that populations do intermingle (Riget et al., 1992; Vis et al., 1997). Tagging experiments in Icelandic waters (Sigurdsson, 1981) included recoveries at long distances east of the release sites (Norway), even to the Barents Sea, also suggesting that there are interactions between the Northwest Atlantic and the Northeast Atlantic populations of Greenland halibut.

The 17 Greenland halibut recovered in Denmark Strait from tagging sites in West Greenland indicated a mix between West and East Greenland stocks, confirming previous work, especially tagging studies by Smidt (1969) and Boje[2] who documented recaptured Greenland halibut off western Iceland from releases in the Godthaab and Lichtenau fjords of southern Greenland. Genetic studies and studies using parasites as natural tags (Riget et al., 1992; Boje et al., 1997) have shown that Greenland halibut in the fjords of southwestern Greenland differ considerably from offshore fish in Davis Strait. Riget and Boje (1988) hypothesized that young Greenland halibut in the southernmost coastal areas of western Greenland originate from different spawning grounds than those in the northern part of western Greenland. Larval distribution studies provide additional information on a link between the populations of southwestern Greenland and those of Denmark Strait. Magnusson's[6] data and more recently data on Icelandic 0-group Greenland halibut, 1970–97 (Hjörleifsson[7]) have provided evidence of larvae in a continuous belt from the Icelandic spawning grounds westward along the continental slope of eastern Greenland and southward to Cape Farewell. From pelagic Greenland halibut eggs and larvae in the western and southeastern Greenland areas, Smidt (1969) distinguished two groups of larvae with different growth patterns and hypothesized the intermingling of larvae from two different spawning areas, namely the spawning complex in Davis Strait and the stock west of Iceland (Denmark Strait). These authors have suggested that Greenland halibut eggs and larvae are transported by the East Greenland Current from Denmark Strait to the southernmost areas of western Greenland, a route shown earlier for cod (Tåning, 1937; Buch et al., 1994).

The behavior of Greenland halibut tagged in the fjords of northwestern Greenland is quite remarkable. The majority have remained within 50 km of release sites, even up to eight years after release and very few fish have undergone large-scale migrations of 100 to 500 km. Greenland halibut released from the fjords of northwestern Greenland have never been reported outside the fjord areas, but apparent residency may also be the result of almost no fishing activity in Baffin Bay (area adjacent to Uummannaq and Upernavik fjord). However, an assumed spawning migration to Davis Strait, is not plausible because a considerable fishery has developed in this area since the late 1980s (Anonymous, 1998). My data are consistent with the general assumption that Greenland halibut in the fjords of northwestern Greenland are recruited from the Davis Strait spawning stock (Smidt, 1969, 1998; Riget et al., 1989) and that adults thereafter remain resident in the fjords, i.e. do not undertake any significant spawning

[6] Magnusson, J. 1977. Notes on eggs and larvae of Greenland halibut at Iceland. ICES (International Council for the Exploration of the Sea) C.M. 1977/F:47, 6 p. ICES, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

[7] Hjörleifsson, E. 1999. Personal commun. Marine Research Institute, P.O. Box 1390, Skúlagata 4, IS-l21 Reykjavík, Iceland.

migrations. Some spawning and spent specimens have been observed in the fjords (Smidt, 1969; Riget et al., 1989; Nielsen and Boje[8]) and therefore spawning may occur in the fjords, at least sporadically. However, low bottom temperatures in the fjords probably inhibit the maturation process (Jensen, 1935; Templeman, 1973).

The seasonality apparent in local migrations for fish in the fjords of northwestern Greenland (Fig. 4) is presumed to correlate with feeding behavior. Allthough information is not available on the seasonality of prey organisms for Greenland halibut in the fjords, seasonal patterns for primary production are expected to affect other trophic levels in the food chain. Seasonality is reflected in the practices of the fishery; it tends to be concentrated in the inner part of the fjords during summer and more dispersed during winter near cities and human settlements (Simonsen and Boje[5]).

Davis Strait tagging data demonstrated that Greenland halibut within this area migrate widely and show no distinct patterns in orientation of movement. Such movements could be associated with spawning as suggested by Bowering (1984), i.e. a northward migration of Greenland halibut tagged in Newfoundland and Labrador to a proposed spawning area in Davis Strait. Jørgensen (1997) also found indications of movements during six years of a survey series, which he interpreted as seasonal movements between feeding areas and spawning grounds in the eastern part of Davis Strait. The wide migrations of offshore Greenland halibut as observed in the present study, i.e. within Davis Strait and from Davis Strait and Godthaab Fjord to Newfoundland, lend support to a proposed relationship between adult movements and spawning behavior.

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[8] Nielsen, J. G., and J. Boje. 1995. Sexual maturity of Greenland halibut at West Greenland based on visual and histological observations. NAFO (Northwest Atlantic Fisheries Organization) SCR Doc. 95/18, ser. no. N2525, 7 p. NAFO Secretariat, 2 Morris Drive, P. O. Box 638, P. O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

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Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples

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Abstract–Marine mammal diet is typically characterized by identifying fish otoliths and cephalopod beaks retrieved from stomachs and fecal material (scats). The use and applicability of these techniques has been the matter of some debate given inherent biases associated with the method. Recent attempts to identify prey using skeletal remains in addition to beaks and otoliths are an improvement; however, difficulties incorporating these data into quantitative analyses have limited results for descriptive analyses such as frequency of occurrence. We attempted to characterize harbor seal (*Phoca vitulina*) diet in an area where seals co-occur with several salmon species, some endangered and all managed by state or federal agencies, or both. Although diet was extremely variable within sampling date, season, year, and between years, the frequency and number of individual prey were at least two times greater for most taxa when prey structures in addition to otoliths were identified. Estimating prey mass in addition to frequency and number resulted in an extremely different relative importance of prey in harbor seal diet. These data analyses are a necessary step in generating estimates of the size, total number, and annual biomass of a prey species eaten by pinnipeds for inclusion in fisheries management plans.

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Increases in marine mammal populations in Washington and Oregon have coincided with decreases in wild salmon populations in these and other western states. Recently, several salmon stocks in the western U.S. have been listed as threatened, endangered, or are under status review. These include coastal Oregon coho (*Onchorhyncus kisutch*), upper Columbia River steelhead (*O. mykiss*), and Snake River spring and fall chinook (*O. tshawytscha*), steelhead, and sockeye salmon (*O. nerka*; NMFS, 1997). Salmon often co-occur with marine mammals and predation may substantially reduce fish populations (Gearin et al., 1986). In these circumstances, an understanding of pinniped diet becomes necessary for the management of endangered fish populations. In 1994, the National Marine Mammal Laboratory began a project to quantify harbor seal (*Phoca vitulina*) predation on salmon in the lower Columbia River and to incorporate marine mammals in salmonid population models. Harbor seals are the most abundant pinniped in the lower river and annual maximum counts can exceed 2000 on the largest haul-out site, a tidal sandbar adjacent to Astoria, Oregon.

Pinniped prey are typically identified from fish sagittae (otoliths) recovered from fecal material (scat) and stomach contents (Brown, 1980; Harvey, 1989; Peirce and Boyle, 1991; Ochoa-Acuña and Francis, 1995; Beach et al.[1]). These methods yield biased results because of partial or complete digestion of otoliths and because of greater probabilities of recovering otoliths from larger individuals and species with robust otoliths and of identifying otoliths of species with distinctive morphological characteristics (Harvey, 1989; Gates and Cheal, 1992; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000). Estimates of harbor seal predation on adult salmonids are particularly poor due to extremely low recovery (because the otoliths are small and fragile) and because harbor seals may not completely ingest large prey and thus otoliths may not be ingested (Pitcher, 1980; Harvey, 1989; Boyle et al., 1990; Harvey and Antonelis, 1994; Cottrell et al., 1996; Riemer and Brown, 1997).

We describe harbor seal diet on the lower Columbia River during spring, summer, and fall from 1) otoliths and 2) other skeletal elements (cranial bones, vertebrae, teeth, gill rakers, etc.) to examine potential differences in the diet characterized by the two methods. In previous studies, identification of all

[1] Beach, R. J., A. C. Geiger, S. J. Jefferies, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC (Northwest Alaska Fisheries Science Center) processed rep. 85-03, 316 p. NWAFC, National Marine Fisheries Service, Seattle, WA.

skeletal elements resulted in at least two times greater frequency of occurrence of some prey taxa than frequencies exclusively derived from otoliths (Riemer and Brown, 1997; Boyle et al., 1990; Cottrell et al., 1996). For major prey taxa, we estimated frequency of occurrence and minimum number of individuals from fish otoliths and other skeletal remains recovered from scats and average mass from otoliths.

Methods

During 1995, 1996, and 1997, scats were collected from Desdemona Sands (river km 26, 123°52′W,46°13′N), the largest harbor seal haul-out site in the lower Columbia River (Huber[2]). Scats were collected intermittently during 1995. From March through August 1996 and from March through October 1997, we attempted to collect 50 harbor seal scats every two weeks at extreme low tides. This sampling period coincided with Columbia River runs of spring, summer, and fall chinook salmon. Scats were collected from haul-outs, and upon arrival at the laboratory were rinsed in nested sieves (2-mm, 1-mm, and 0.5-mm mesh width). All skeletal elements were recovered, dried, and stored in vials. Cephalopod remains were stored in 70% isopropyl or ethyl alcohol. Other invertebrate remains were relatively rare (≤2% frequency of occurrence) and their contribution to the diet was disregarded because of difficulties enumerating individuals and determining primary from secondary (prey within large, ingested fishes) prey. Otoliths were identified to lowest possible taxon, their anatomical location recorded (left or right side), and enumerated (number for left side and number for right side). Lengths of intact left or right otoliths were measured parallel to the sulcus to the nearest 0.1 mm with an ocular micrometer. Micrometer measurements were verified with hand-held calipers. Other skeletal structures (such as teeth, vertebrae, and cranial bones) were identified to lowest possible taxon by comparing prey remains to reference samples (NMML[3]).

Scat collections were divided into three seasons: spring (samples collected prior to 15 May), summer (samples collected from 15 May to 15 July), and fall (samples collected after 15 July). These dates distinguish runs of spring, summer, and fall chinook salmon crossing the Bonneville Dam (river km 235), less two weeks estimated for travel from the lower Columbia River (Fryer, 1998). For each season, harbor seal diet was described by frequency of occurrence (FO), minimum number of individuals (MNI), and average prey mass estimated from otoliths of all major prey taxa. Frequency of occurrence (FO) of prey taxon j in season k was defined as

$$FO_{jk} = \frac{\sum_{i=1}^{s_k} O_{ijk}}{s_k},$$

where O_{ijk} = a binary variate indicating presence (1) or absence (0) of taxon j in sample i in season k; and

s_k = the total number of scats containing identifiable prey remains in season k.

Rare prey taxa were grouped with similar taxa for analyses. Unknown prey remains that were clearly distinct from known taxa were considered "unidentified taxa" in samples containing "identified" hard parts. Scats containing skeletal remains considered "unidentifiable," i.e. extremely eroded bone or fragmented material, were excluded from analyses. The minimum number of individuals (MNI) was estimated from the greatest number of left or right otoliths and unique or paired bone structures and expressed within each season as total MNI or average MNI per scat (total MNI/number of scats collected). Presence of non-unique fish remains (non-unique vertebrae, gillrakers, teeth) constituted a single individual. For example, if a scat sample contained five left otoliths, three right otoliths, and six atlas or axis vertebrae of a prey taxon, the MNI was six. FO and MNI were calculated from otoliths and again from all prey remains. Prey masses were estimated for the three seasons from allometric relationships between otoliths and body size (Harvey et al., 2000; Table 1). If relationships were unavailable for a species, regressions generated for a similar species were used. Otolith lengths were multiplied by a species-specific correction factor when available or an average correction factor to account for reduction in length due to digestion (Harvey, 1989). All intact left or right otoliths of a prey taxa were measured, and estimated masses were averaged for each season.

Suitable morphometric regressions were not available for several salmon species or did not include juvenile fish; therefore, we generated regressions including subadult age classes specifically for our study. In addition to published regressions, relationships between salmon otoliths and fish mass used in this study were calculated from National Marine Mammal Laboratory reference samples, the private collections of Walker[4] and NRC[5] (Table 1). Because of the large discrepancy in masses of adult and juvenile salmonids, otoliths were identified to species and classified as adult or juvenile according to species-specific lengths estimated from regression equations. "Adults" described all returning upriver migrants, including reproductively mature individuals and jacks. "Juveniles" were seaward migrants and may have included two-year-old fish of some species (Groot and Margolis, 1991). *Onchorhyncus*

[2] Huber, H. R. 1997. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] NMML (National Marine Mammal Laboratory). 1997. Marine Mammal Prey Osteological Reference Collection. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[4] Walker, W. 1998. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[5] NRC (National Resources Consultants). 1998. Unpubl. data. Natural Resources Consultants, Inc., 4055 21st Ave. W, Suite 100, Seattle, WA 98119.

Table 1

Predicted standard length ($L=a+bx$; L=estimated standard length [cm], x=otolith length [mm]) and weight ($W=cL^d$; W=estimated weight [g], L=estimated standard length) of common harbor seal prey and sources of data. Calculations for groups of fish are based on species (in parentheses). Sockeye salmon calculations are based on regressions for silver salmon.

		Length		Weight		
Taxon	Species	a	b	c	d	Source
Ammodytidae	Pacific sand lance	0.727	0.137	0.0529	3.46	NMML[1]
Clupeidae	Pacific herring	–1.85	5.24	0.0044	3.398	Harvey et al., 2000.
	American shad	–11.08	11.46	0.0135	3.046	Harvey et al., 2000.
Cottidae	Pacific staghorn sculpin	–2.26	2.58	0.011	3.229	Harvey et al., 2000.
Embiotocidae	shiner surfperch	–0.52	1.74	0.01	3.515	Harvey et al., 2000.
Engraulidae	northern anchovy	0.85	2.28	0.0485	2.413	Harvey et al., 2000.
Gadidae	Pacific hake	0.96	2.04	0.0081	2.966	Harvey et al., 2000.
Gadidae	Pacific tomcod	–3.51	1.77	0.0064	3.191	Harvey et al., 2000.
Hexagrammidae	Hexagrammids (lingcod)	–6.03	8	0.0023	3.567	Harvey et al., 2000.
Osmeridae	whitebait smelt	3.02	2.11	0.0063	3.233	Harvey et al., 2000.
	eulachon	–2.7	4.71	0.0077	3.075	Harvey et al., 2000.
Pleuronectidae	Dover sole	12.23	2.75	0.0094	3.092	Harvey et al., 2000.
	English sole	–2.76	3.82	0.0163	2.939	Harvey et al., 2000.
	rex sole	–2.5	4.8	0.0238	2.692	Harvey et al., 2000.
	slender sole	1.08	3.37	0.0058	3.293	Harvey et al., 2000.
	starry flounder	0.23	3.35	0.0107	3.268	Harvey et al., 2000.
Salmonidae	chinook salmon	–10.4	6.73	0.0043	3.207	length: Walker[2]; weight: NRC[3]
	cutthroat trout	–91.2	89.3	0.0155	2.97	Walker[2]
	silver salmon	3.29	9.33	0.0103	3.092	length: NRC[3]; weight: Harvey et al., 2000.
	sockeye salmon (silver salmon)	3.29	9.33	0.0103	3.092	length: Walker[2]
	steelhead salmon	–32.43	14.77	0.0275	2.895	Harvey et al., 2000.
Scorpaenidae	rockfishes (black rockfish)	8.7	1.6	0.1225	2.499	Harvey et al., 2000.
Stichaeidae and Pholididae	gunnel and prickelback (wattled eelpout)	12.42	5.22	0.0007	3.483	Harvey et al., 2000.
	gunnel and prickelback (Pacific sand fish)	–4.57	6.06	0.0171	2.953	Harvey et al., 2000.

[1] NMML (National Marine Mammal Laboratory). 1997. Marine Mammal Prey Osteological Reference Collection. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA. 98115.

[2] Walker, W. 1998. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115.

[3] NRC (National Resources Consultants, Inc.). 1998. Unpubl. data. National Resources Consultants, Inc. 4055 21st Ave. W, Suite 100, Seattle, WA, 98119.

clarki, *O. kisutch*, *O. nerka*, and *O. mykiss* less than 30 cm in length and *O. tshawytscha* less than 35 cm in length were considered seaward migrating juveniles (Groot and Margolis, 1991). All distinguishable salmon otoliths were identified to species and all identifications were verified by W. Walker.

Annual and seasonal variations in frequency of occurrence (FO) were examined with generalized linear models (Venables and Ripley, 1994). We limited our analyses to prey taxon with FO >5% during one or more seasons. Frequency of occurrence on each sampling date was modeled as a binomial random variable and for each prey taxon, we fitted five models: constant, season (S), year (Y), season+year ($S+Y$), and season+year with interactions ($S\times Y$). To account for overdispersion, we scaled Akaike's information criterion (AIC) using b=residual deviance/degrees of freedom from the $S\times Y$ model (Venables and Ripley, 1994). The model with the smallest scaled AIC was considered the best descriptor of seasonal and annual variation in FO.

Results

Over 1500 scats were collected from March 1995 through October 1997. Sample sizes varied among years and within season (Table 2). Frequency and number of indi-

Table 2

Sample collection dates, harbor seal scats with some identifiable prey remains, without any identifiable remains, and without remains for samples collected from Desdemona Sands 1995 through 1997. Spring (<15 May), summer (15 May to 15 July), and fall (>15 July) designate timing of chinook salmon runs on the Columbia River.

		Harbor seal scats		
Season	Collection date	With identifiable remains	Without identifiable remains	Without remains
Spring	5 Mar 1995	13	1	0
	5 Mar 1995	29	2	0
	14 Mar 1996	29	1	1
	21 Mar 1996	11	1	1
	10 Apr 1996	42	4	0
	2–8 May 1996	44	2	1
	11 Mar 1997	16	1	0
	26 Mar 1997	7	4	0
	10–11 Apr 1997	29	7	1
	15 Apr 1997	22	6	0
	28 Apr–1 May 1997	28	4	11
	9–10 May 1997	45	6	12
	Subtotal	315	39	27
Summer	18–19 May 1995	53	1	4
	14–16 Jun 1995	81	1	0
	28–29 Jun 1995	78	1	0
	14 Jul 1995	32	3	0
	30–31 May 1996	53	2	1
	18–19 Jun 1996	50	1	1
	2 Jul 1996	52	3	0
	27 May 1997	34	6	10
	6 Jun 1997	24	8	0
	23 Jun 1997	47	8	9
	8 Jul 1997	74	2	1
	Subtotal	578	36	26
Fall	15 Aug 1996	78	1	0
	29 Aug 1996	59	2	0
	22 Jul 1997	64	5	6
	4 Aug 1997	102	1	0
	19 Aug 1997	56	1	0
	3 Sep 1997	51	5	0
	16 Sep 1997	41	6	0
	16–17 Oct 1997	41	6	0
	Subtotal	492	27	6
	Total	1385	102	59

viduals consumed by harbor seals on the Columbia River were extremely variable, even among sample collections fewer than two weeks apart. Effort and sample sizes were unequal for season and years but we chose to include all data to better describe harbor seal diet. More than 45 prey taxa were described in 1385 samples with identifiable prey remains; however, most of the diet by number and frequency was composed of about 17 prey taxa (Table 3). Seasonal effects were important for 15 of 17 harbor seal prey with FO ≥5% (Table 3). Annual effects also were important for FO of lamprey (*Lampetra* spp.), Pacific hake (*Merluccius productus*), and northern anchovy (*Engraulis mordax*), and year-season interactions were included for three prey taxa (Table 3). All taxa had variances of FO greater than predicted by a binomial model (over-dispersion values, $b>1$; Table 3).

Table 3

Total minimum number of individuals (MNI), frequency of occurrence (FO), significant differences in frequency of occurrence of major prey taxa identified from all skeletal remains recovered from harbor seal scat (*S* indicates season, *Y* indicates year, *S*×*Y* indicates interaction, and N indicates no effects), and an estimate of over-dispersion of the binomial model (*b*). Only taxa with FO. >0.05 in at least one season were examined.

	MNI (all remains)			FO (all remains)				
Prey taxon	Spring	Summer	Fall	Spring	Summer	Fall	Effect	*b*
Pacific herring	168	511	141	0.36	0.57	0.22	*S*	8.4
Pacific staghorn sculpin	256	170	284	0.41	0.19	0.25	*S*×*Y*	2.4
Smelt species	133	204	625	0.28	0.18	0.35	*S*	6.2
Pacific tomcod	66	73	251	0.18	0.09	0.39	*S*	7.2
Lamprey species	109	204	41	0.26	0.25	0.06	*S*+*Y*	2.0
Starry flounder	136	105	160	0.30	0.14	0.12	*S*×*Y*	2.7
American shad	36	108	116	0.11	0.19	0.22	*N*	6.1
Other flatfish	102	129	132	0.20	0.12	0.18	*S*	2.2
Pacific hake	30	72	136	0.09	0.12	0.28	*S*+*Y*	4.0
Shiner surfperch	26	131	69	0.07	0.18	0.08	*S*	2.2
Gunnel and prickelback	47	55	30	0.15	0.08	0.06	*S*	3.0
Juvenile salmonids	92	71	30	0.19	0.05	0.05	*S*	3.2
Northern anchovy	3	63	290	0.01	0.06	0.19	*S*+*Y*	2.9
Adult salmonids	22	33	50	0.06	0.04	0.10	N	4.6
Peamouth chub	12	63	41	0.03	0.08	0.05	*S*×*Y*	2.4
Pacific sand lance	37	18	11	0.10	0.03	0.02	*S*	1.5
Rockfish species	23	14	18	0.07	0.02	0.03	*S*	1.5

The inclusion of all skeletal elements recovered from scat increased the MNI and FO of all harbor seal prey taxa (Table 4). The FO more than doubled for most taxa and usually was more affected by including all prey elements than was the average MNI (Table 4). We compared the MNI of several common harbor seal prey estimated from all structures to an estimate based on the number of recovered otoliths multiplied by a species-specific correction factor for recovery rate (accounting for complete digestion of the otolith; Harvey, 1989, Fig. 1). A value of 1.0 indicated that the same estimate was derived from both methods, whereas 0.5 indicated that the MNI estimated from all structures was twice the estimate from otoliths.

Seasonal variation was also apparent in estimated prey mass (Table 5). In some instances, estimates were based on very few otolith measurements, values were taken from the literature, or mass was averaged from other seasons when no intact otoliths were recovered (Table 5). Because some species were difficult to discern or regression relationships were unavailable, species were grouped by phylogeny or size similarities (Table 5). Smelts (Osmerids) were pooled by family and mass was estimated from whitebait smelt (*Allosmerus elongatus*), the most abundant species by distinguishable otoliths, and eulachon (*Thaleichthys pacificus*), although longfin smelt (*Spirinchus thaleichthys*) and surf smelt (*Hypomesus pretiosus*) were occasionally identified in harbor seal scats. Although smelt otoliths could be distinguished by species, smelt bone could not. Smelt mass estimates were based on eulachon (in their relative proportion) and whitebait smelt because although less common than the other three similar size species, eulachon were much larger. Masses of juvenile and adult salmonids were estimated separately for five species identified in harbor seal scat, with the exception of sockeye salmon, which was represented by one otolith from an adult fish. Mass for sockeye was based on regressions generated for silver salmon. Cutthroat (*Onchorhyncus clarki)* and steelhead salmon *(O. mykiss)* were not often distinguishable by otoliths, and mass estimates were based on steelhead because of their numerical dominance in the lower Columbia River. The sticheid-pholid group included fish from a variety of families: three spine stickleback (*Gasterosteus aculeatus*), snake prickleback (*Lumpenus sagitta*), high cockscomb (*Anoplarchus purpurescens*), wattled eelpout (*Lycodes palearis*), Pacific sandfish (*Trichodon trichodon*), and saddleback gunnel (*Pholis ornata).* Although not taxonomically related, these species were seldom represented by otoliths, individuals were very small, and with the exception of gunnels, were rare by number and frequency (Table 4). Little has been published about relationships between otolith length and fish length or fish length and mass for

Table 4

Average minimum number of individuals (MNI) per scat (total number of individuals identified in all scats collected in a season/ total number of scats collected in a season) and frequency of occurrence (FO) for all skeletal remains and for otoliths exclusively for major prey taxa of harbor seals in the Columbia River during spring, summer, and fall. All = all skeletal remains.

	Spring				Summer				Fall			
	Average MNI/scat		FO		Average MNI/scat		FO		Average MNI/scat		FO	
Prey taxa	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths	All	Otoliths
American shad	0.11	0.01	0.11	0.01	0.19	0.01	0.19	0.01	0.24	0.03	0.22	0.02
Cephalopod	0.01		0.01		0.02		0.02		0		0	
Elasmobranch	0.08		0.07		0.01		0.01		0.01		0.01	
Gunnel and prickelback	0.15	0	0.15	0	0.10	0	0.08	0	0.06	0	0.06	
Hexagrammid	0.02	0	0.02	0	0.01	0	0.01	0	0.03	0	0.03	
Lamprey species	0.35		0.26		0.35		0.25		0.08		0.06	
Northern anchovy	0.01	0	0.01	0	0.11	0.06	0.06	0.02	0.59	0.52	0.19	0.10
Other flatfish	0.41	0.25	0.20	0.07	0.16	0.03	0.12	0.03	0.28	0.12	0.18	0.06
Pacific hake	0.10	0.02	0.09	0.01	0.12	0.01	0.12	0.01	0.28	0.02	0.28	0.02
Pacific herring	0.53	0.24	0.36	0.09	0.88	0.52	0.57	0.21	0.29	0.16	0.22	0.09
Pacific mackerel	0.02	0	0.02	0	0	0	0	0	0.01	0	0.01	0
Pacific sand lance	0.12	0.06	0.10	0.04	0.03	0.01	0.03	0.01	0.02	0.02	0.02	0.01
Pacific staghorn sculpin	0.81	0.62	0.41	0.20	0.29	0.17	0.19	0.08	0.58	0.42	0.25	0.11
Pacific tomcod	0.21	0.09	0.18	0.06	0.13	0.05	0.09	0.02	0.51	0.24	0.39	0.13
Peamouth	0.04	0.02	0.03	0.01	0.11	0.06	0.08	0.03	0.08	0.05	0.05	0.02
Rockfish species	0.07	0.02	0.07	0.02	0.02	0.01	0.02	0	0.04	0.01	0.03	0.01
Salmon species—adult	0.07	0.04	0.06	0.03	0.06	0.04	0.04	0.02	0.10	0.02	0.10	0.01
Salmon species—juvenile	0.29	0.16	0.19	0.06	0.12	0.10	0.05	0.02	0.06	0.02	0.05	0.01
Shiner surfperch	0.08	0.04	0.07	0.02	0.23	0.15	0.18	0.05	0.14	0.10	0.08	0.04
Smelt species	0.42	0.31	0.28	0.12	0.35	0.30	0.18	0.11	1.27	1.21	0.35	0.21
Starry flounder	0.43	0.24	0.30	0.11	0.18	0.09	0.14	0.05	0.33	0.28	0.12	0.06
Unidentified flatfish	0.04	0.02	0.03	0	0.02	0	0.02	0	0.02	0	0.02	0

these families; rather than ignore their occurrence, these species were pooled and mass estimates were based on measurements of wattled eelpout and sandfish otoliths (Table 5). The family Scorpaenidae was composed mostly of juvenile fish (*Sebastes* and *Sebastelobus* spp.) which can seldom be distinguished to species from bones and otoliths. Mass estimates were based on black rockfish (*Sebastes melanops*; Table 5). Morphometeric relationships for peamouth (*Mylocheilus caurinus*) were unavailable in the literature. Peamouth are small, slender members of the minnow family, less than 36 cm in length, with a shape similar to several other small harbor seal prey. Mass was assumed to be less than 100 g. Hexagrammids included lingcod (*Ophiodon elongatus*) and greenlings (*Hexagrammos* spp.) also were poorly represented by otoliths. Mass was estimated from lingcod otoliths (Table 5). Because bones and otoliths were often difficult to identify to species, flatfish other than starry flounder were pooled and mass was calculated from the average of estimated masses of identified otoliths (rex sole, *Glyptocephalus zachirus*; English sole, *Pleuronectes vetulus*; Dover sole, *Microstomus pacificus*; rock sole, *Pleuronectes bilineatus*; slender sole, *Eopsetta exilis*) for each season. In contrast, starry flounder remains were easily identified and much more abundant than any other flatfish species (Table 4).

Several taxa were not represented by otoliths because they were completely digested or because the species lacked otoliths. No intact Pacific mackerel (*Scomber japonicus*) otoliths were recovered from scat and their mass was assumed to be less than 700 g, the upper limit reported by Eschmeyer and Herald (1983). Lamprey species included river (*Lampetra ayresii*) and Pacific lamprey (*L. tridentata*). Mass was estimated from the upper limit of outgoing Pacific and river lamprey from Pacific Northwest river systems (Beamish, 1980). Little information was available for predicting the mass of elasmobranchs; however, all elasmobranchs (spiny dogfish, *Squalus acanthias;* and skates, Rajidae) consumed by harbor seals appeared to be juveniles. Elasmobranch mass was extrapolated from a regression of vertebral centrum width on mass from another skate species (Zeiner and Wolf, 1993), yielding an upper estimate of 490 g. We assumed the mass of skates and spiny dogfish consumed by harbor seals to be of a similar size, and all less than 500 g. Cephalopod (*Loligo*

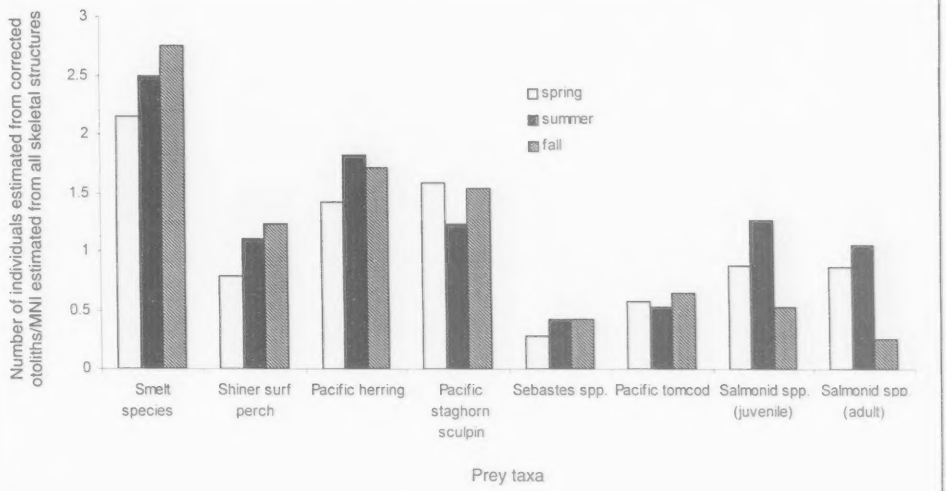

Figure 1

For eight prey taxa, ratio of estimated mean number of individuals estimated from the number of otoliths recovered from scat multiplied by a species-specific correction factor for recovery rate (Harvey, 1989) to MNI estimated from all structures recovered from harbor seal scats collected from Desdemona Sands during spring, summer, and fall 1995 through 1997. Values for smelt species are based on correction factors for eulachon. Values for salmonid species are based on correction factors for steelhead salmon.

opalescens and *Octopus* spp.) mass was estimated from regressions of beak measurements on mantle length and mass (Wolf, 1982).

Discussion

Diet of harbor seals in the Columbia River

Identification of prey remains indicated that the diet of harbor seals in the Columbia River was temporally variable and seals appeared to exploit prey when species were abundant. Many of the dominant prey by number and frequency were small fish such as herring, smelts, northern anchovy, juvenile flatfish, and sculpins (Tables 3 and 4). Pacific herring, Pacific staghorn sculpin (*Leptocottus armatus*), and smelts were three of the top six prey taxa by number and frequency for all three seasons (Table 4), although estimated masses varied greatly between season, indicating that seals preyed on different size classes (Table 5). Interestingly, scats without remains were most common during late spring and summer (Table 2). Olesiuk et al. (1990) reported similar results from British Columbia and suggested harbor seals were feeding on soft-bodied prey and roe. Occurrence of these scats in our study coincided with pupping on the lower Columbia River (Huber[6]), but an alternative explanation is that these may have been from nursing pups.

Most common harbor seal prey were variable by season or year (or both). Seasonal effects in the diet indicated periods when prey were reproducing, when young of the year were available, or perhaps an absence of highly abundant prey when seals relied more heavily on consistently available species. Annual differences in frequency of occurrence may have been largely the result of differences in sample timing or prey cohort strength (Moyle and Cech, 1982; Dark and Wilkins, 1994). Significant year and interactive effects between season and year probably reflected differences in prey year class (Table 3). For example, FO of anchovy (known to have high variability in recruitment) collected during fall of 1996 was 63%, whereas during fall of 1997 it was only 2%, although samples were collected on similar dates (Table 1). Harbor seals are generalist feeders and differences in frequency and number of prey probably reflect the temporal availability of prey rather than predator selection. This hypothesis is supported by AIC over-dispersion constants (b) greater than 1.0 for all prey taxa (Table 3). A binomial model assumes constant probabilities of a prey taxon occurring in scats collected on any sampling date within a season or year. Ephemerally abundant prey will have highly variable probabilities of occurrence in harbor seal scats collected in each season. It is likely that the overdispersion constant underestimates deviations for taxonomic groups, including more than one species such as salmonids and smelts, because temporal abundance of the different species in the group may be offset.

[6] Huber, H. R. 1997. Unpubl. data. National Marine Mammal Laboratory, 7600 Sand Point Way, NE, Bldg. 4, Seattle, WA 98115.

Table 5

Average mass (g) of harbor seal prey, standard deviation (SD), and number of otoliths measured (*n*) for spring, summer, and fall prey of harbor seals in the Columbia River. Boldface values are estimates calculated from other seasons (when no intact otoliths were recovered within a season) or from literature sources (when no structures were available for measurement).

		Spring			Summer			Fall		
Family	Prey taxa	Avg. mass	SD	*n*	Avg. mass	SD	*n*	Avg. mass	SD	*n*
Clupeidae	American shad	198	22	4	517	601	5	523	284	11
	Pacific herring	93	35	50	96	64	238	97	73	54
Engraulidae	Northern anchovy	9		1	12	2	30	14	5	192
Osmeridae	Smelt species	15	23	84	6	2	147	7	3	331
Gadidae	Pacific tomcod	128	115	24	180	106	25	228	132	107
	Pacific hake	67		1	421		1	446	292	2
Pleuronectidae	Starry flounder	70	117	64	114	243	52	89	168	101
	Other flatfish	181	100	35	181	111	42	225	82	35
Cottidae	Pacific staghorn sculpin	140	84	136	160	84	88	115	42	45
Salmonidae	Chinook juvenile	206	150	22	41	93	21			0
	Chinook adult	1385		1	8515	6854	2	6862	1757	4
	Cutthroat juvenile	225	56	7	255	66	6	315		1
	Cutthroat adult	509	51	7	426	52	2			0
	Silver juvenile	277		1			0	88	103	2
	Silver adult	1607	983	2	671	241	15	4317	3545	3
	Steelhead juvenile	488		1	283	81	2			0
	Steelhead adult	1637		1	897		1			0
	Sockeye adult	2832		1			0			0
Embiotocidae	Shiner surfperch	79	39	7	85	43	80	79	42	45
Stichaeidae and Pholididae	Gunnels and prickelbacks	**90**	**84**	0	97	38	3	84	127	3
Hexagrammidae	Hexagrammids	**2090**	**1727**	0	3410	1375	2	756	135	2
Scorpaenidae	Rockfish species	187	87	6	132	7	2	114		1
Ammodytidae	Pacific sand lance	72	63	3	62	58	8	151		1
Elasmobranchs	Elasmobranchs	**500**		0	**500**		0	**500**		0
Scombridae	Pacific mackerel	**700**		0	**700**		0	**700**		0
Petromyzontidae	Lamprey species	**50**		0	**50**		0	**50**		0
Ptychocheilus	Peamouth chub	**100**		0	**100**		0	**100**		0
Cephalopods	Cephalopods	**21**	**1**	0	**21**	**1**	0			0

Salmon in the harbor seal diet

Harbor seals consumed several species and sizes of salmon throughout our study, but frequency was greatest during spring. Size of otoliths recovered indicated that most of these fish were juvenile chinook and that adult salmon were consumed to a lesser extent, primarily during fall. Fryer (1998) reported no difference in mean fork lengths of adult spring–summer *O. tshawytscha* with scars from pinnipeds and those without scars at the Bonneville Dam and observed a greater percentage of fish with scars earlier in the year, although these findings do not necessarily contradict data from our study. Scarred fish represent failed predation and perhaps harbor seals attempted to capture fish beyond their ability when spring run-off results in greater water turbidity. In addition, part of the discrepancy may be due to the classification of "adult" salmon. For our purposes, we categorized all fish with estimated lengths greater than outgoing migrants (30 to 35 cm depending on the species) as "adults." The mean lengths of scarred spring-summer *O. tshawytscha* from 1994 to 1996 (75.9 to 79.3 cm standard length) were greater than the mean length of "adult" fish estimated from prey remains (73.4 cm mean standard length).

Riemer and Brown (1997) also examined all skeletal structures; however, their results summarized data for four years and 154 samples collected on eight dates. Riemer and Brown (1997) reported salmon FO as great as 39% for a single sampling date but found no salmonid remains in scats collected during February and March.

Table 6

Harbor seal prey taxa ranked by minimum number of individuals (MNI) estimated from all skeletal structures and otoliths, frequency of occurrence (FO) estimated from all skeletal structures and from otoliths, and average mass of prey estimated from allometric relationships between otoliths and fish size. Prey are ranked for all seasons; i.e. smelt are the most numerically abundant prey over spring, summer, and fall. Data (as opposed to ranks) are presented in Tables 4 and 5.

Prey taxa	MNI all	MNI otoliths	FO all	FO otoliths	Mass
Smelt species	1	1	3	1	21
Pacific staghorn sculpin	2	2	1	2	10
Pacific herring	3	4	1	3	15
Starry flounder	4	6	5	5	16
Other flatfish	5	7	8	7	7
Lamprey species	5		5		19
Pacific tomcod	7	7	5	6	8
American shad	8	15	4	14	4
Shiner surfperch	9	7	10	8	18
Pacific hake	10	14	9	14	
Salmon species—juvenile	11	10	12	10	6
Northern anchovy	12	3	15	4	20
Gunnel and prickelback	13		11		17
Cephalopod	14		13		13
Pacific mackerel	15		14		3
Salmon species—adult	16	12	15	12	1
Peamouth	16	11	17	11	12
Pacific sand lance	18	13	18	13	14
Rockfish species	19	16	19	8	10
Unidentified flatfish	20	4	20		
Elasmobranch	21		21		5
Hexagrammid	22		22		2

Monthly FOs were based on a single sampling collection. During our study, FO of juvenile salmon was 50% on a sampling date during March of 1997; however, no salmon remains were found in scats collected a week earlier during 1995. Additionally, we found salmonid remains in harbor seal scat during every month of our data collection and we found no significant differences in the seasonal occurrence of adult salmonids. This finding, however, may have been due to our grouping species.

Harbor seals eat Columbia River salmon; however, they feed mostly on juvenile fish during the spring, and otolith identifications have indicated that most of these are chinook salmon. Currently, salmonid bone cannot be identified to species; however, the National Marine Mammal Laboratory is investigating identification of salmonid species from skeletal remains by using genetic techniques.

Comparison of identification methods

Identifying and enumerating prey from all skeletal structures is more time consuming than relying exclusively on otoliths and the described diet may be substantially different. MNI and FO both increase when all structures are used, particularly for taxa such as Pacific tomcod (*Microgadus proximus*), Pacific hake, American shad (*Alosa sapidissima*), salmon spp., hexagrammids, elasmobranchs, and lampreys that are vastly underestimated from otoliths or are entirely lacking in otoliths (Table 4). Relative importance of prey in the diet also may be dramatically affected (Table 6). Prey of the greatest estimated masses are ranked among the least important prey by number and frequency with the use of all skeletal elements and these prey are often completely absent from the diet described from otoliths. If one were to rely solely on otolith identifications, these prey could be entirely overlooked. The extrapolation of estimated biomass of each prey taxa from average mass estimated by otolith length and MNI estimated from all skeletal remains has a variety of caveats—namely, the relative contribution of large, infrequent prey may be vastly underestimated by using otoliths.

Although the identification of all structures increases the magnitude of both MNI and FO, estimates of the number of individual prey are likely to be less accurate. A description of pinniped diet from all prey remains is subject to many of the same biases inherent in otolith identifications. Identification of all skeletal structures assumes an equal probabil-

ity of detecting all prey species and of recovering remains after consumption; these assumptions were violated to some extent in our study because, like otoliths, passage and identification of prey structures are taxon-specific (Harvey, 1989; Cottrell et al., 1996; Marcus et al., 1998). In captive experiments, herring (*Clupea pallasi*) were identified by 11 structures recovered in scats (other than otoliths), whereas smelt were represented only by vertebrae (Cottrell et al., 1996). Smelt vertebrae cannot be used to enumerate individuals, whereas several herring bones commonly recovered in scats are unique or are structures with definite sides (prootics, atlas and axis vertebrae), and even highly eroded herring bone retain characteristics identifiable to species. In contrast, bones of some taxa such as pleuronectids erode rapidly, losing species traits and are identified only to family. Given these factors, the identification of all skeletal structures represents the relative consumption of some prey more accurately than others. Further, MNI estimated from all skeletal structures is not corrected for complete digestion of structures useful for enumerating individuals. To date, there are no correction factors for complete digestion of bones and this lack, doubtlessly, is a source of substantial bias.

Behavior of both predator and prey also affects identification and enumeration of prey remains in scats. Small, schooling fish, such as smelts, are more likely to be consumed in greater numbers than larger, solitary fish such as hexagrammids. Smelts are most frequently identified from vertebrae; therefore MNI is more severely underestimated because more than one individual is likely to be consumed. Captive feeding studies also have indicated that the activity of the pinniped, its meal size, size of prey, and the physical structure of the prey bone all affect passage rate and the degree of erosion (Cottrell et al., 1996; Tollit et al., 1997; Marcus et al., 1998; Bowen, 2000).

The estimation of MNI from all prey structures recovered in scats presents a variety of complications; however, the alternative—using otolith correction factors—also has problems. Otolith correction factors based on recovery rates from feeding experiments are highly variable between repeated trials of the same individuals, different individuals, and different pinniped species (Harvey, 1989; Cottrell et al., 1996; Tollit et al., 1997; Bowen, 2000). Although his results were inconclusive, Bowen (2000) suggested that differences in activity levels may account for much of the variability in digestion (and correction factors). Activity levels among wild harbor seals are likely to be more variable than those between captive harbor seals with and without access to water, and thus otolith correction factors may yield erroneous estimates of individuals consumed by free-ranging predators. Limiting analyses of diet to qualitative measures such as FO will reduce the biases of including bone identification; however, the overall importance of frequent, small prey may be much less than indicated by their relative frequency.

Pinnipeds are considered generalist feeders and may feed on large numbers of abundant, frequently encountered prey; however, if mass is considered a measure of importance, they may be sustained by infrequent, large prey (Tables 4–6). A few prey species were both abundant and frequent (herring, smelts, sculpins, flatfish), yet their estimated masses were small. Large, infrequent species such as lingcod, hake, rockfish, and salmon may contribute more total mass to a hypothetical "meal." Unfortunately, these prey were also poorly represented by otoliths in our study and therefore our mass estimates may be inaccurate.

All methods of examining marine mammal diets, such as fecal analyses, stomach lavage, or stomach content analysis, are inherently biased to some degree. Biases of fecal analyses have been discussed at length in the literature; however, fecal analysis remains the least invasive and least expensive technique and allows for large sample sizes. Identification of all skeletal elements, rather than otoliths exclusively, is an improvement on other techniques. Although results are still subject to biases, prey taxa represented by hard parts in fecal material represent a minimum estimate of prey consumed. In addition, an examination of skeletal elements other than otoliths is mandatory for assessing the impact of harbor seals on certain prey species—protected salmon stocks, for example.

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Pinniped diet composition: a comparison of estimation models

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Abstract—Along the west coast of the United States, the potential impact of increasing pinniped populations on declining salmonid (*Oncorhynchus* spp.) stocks has become an issue of concern. Fisheries managers need species-specific estimates of consumption by pinnipeds to evaluate their impact on salmonid stocks. To estimate consumption, we developed a model that estimates diet composition by reconstructing prey biomass from fecal samples. We applied the model to data collected from harbor seals (*Phoca vitulina*) that are present year-round in the lower Columbia River where endangered stocks of salmonids pass as returning adults and as seaward-migrating smolts. Using the same data, we applied the split-sample frequency of occurrence model, which avoids reconstructing biomass by assuming that each fecal sample represents an equal volume of consumption and that within each sample each prey item represents an equal proportion of the volume. The two models for estimating diet composition yielded size-specific differences in consumption estimates that were as large as tenfold for the smallest and largest prey. Conclusions about the impact of harbor seal predation on adult salmonids, some of their largest prey species, remain uncertain without some appropriate rationale or further information (e.g. empirical captive studies) to discriminate between these models.

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During the last three decades, harbor seal (*Phoca vitulina*) and California sea lion (*Zalophus californianus*) populations along the west coast of the United States have increased dramatically (Forney et al., 2000). During the same period, numerous salmonid (*Oncorhynchus* spp.) stocks that are consumed by these pinnipeds have declined and some of these stocks have been classified as threatened or endangered (NMFS, 1997). To evaluate the impact of pinnipeds, fisheries managers need species-specific estimates of salmonid consumption by pinnipeds.

In some limited situations, pinniped prey consumption can be determined from direct observation if the pinniped brings the prey to the surface and feeding occurs in a few predictable areas (Bigg et al., 1990). However, in most situations, consumption estimates have relied on a less direct approach that uses estimates of pinniped energetic requirements, prey energy density, and pinniped diet composition (Olesiuk, 1993; Hammill et al., 1997; Stenson et al., 1997; Nilssen et al., 2000). In their simplest form, these models express biomass consumption of prey species i as $B_i = \xi\pi_i/\varepsilon_i$, where ξ is the total energy requirement of the pinnipeds, π_i is the proportion of the energy in the diet derived from species i, and ε_i is the energy density (kcal/g) of species i. The total energy requirement of a population depends on the size of the population and requirements of each seal, which vary by sex, age, and status (i.e. whether it is molting, pregnant, lactating). If prey energy density is constant or an average energy density is used, biomass consumption can be expressed as $B_i = \xi\pi_i$, where ξ is the total biomass requirement and π_i is the proportion of the biomass derived from species i. Valid estimates of pinniped energetic requirements and prey energy density are important, as well as accurate estimates of pinniped diet composition.

Diet composition can be determined from skeletal remains in scat (feces) and from stomach and intestinal contents, or stomach lavage. Each of these methods has some inherent bias (Bigg and Perez, 1985; Pierce et al., 1991). Examination of prey remains in scat is noninvasive and allows for the largest sample size. There are, however, numerous well-recognized problems in describing marine mammal diet from scats (Jobling, 1987; Harvey, 1989; Harvey and Antonelis, 1994; Tollit et al., 1997b; Marcus et al., 1998). In particular, nonrandom passage of hard parts, primarily otoliths, biases estimates of diet composition; however, the bias can be reduced by inclusion of all hard parts (e.g. bones) (Browne et al., 2002).

In 1994, we began an investigation of harbor seal consumption of salmonids in the lower Columbia River. Initial attempts to survey the lower 110 km stretch of the river to estimate adult salmonid consumption by direct observation proved infeasible. The only remaining noninvasive alternative was to develop a consumption estimate

based on analysis of scat collections. During 1995–97, harbor seal scats were collected at the Desdemona Sands haulout from 1 March to 15 October. By combining diet composition obtained from scat analysis and contemporaneous surveys of seal abundance, we estimated the average consumption of salmonids and other prey in the Columbia River by harbor seals during spring, summer, and fall of 1995–97.

In our study, we focussed on the method of estimating diet composition from a sample of scats. We describe an estimator for diet composition based on reconstruction of the prey biomass represented in the scat and show how it is related to an alternative estimator described by Olesiuk (1993). Using the data collected on harbor seals in the Columbia River, we demonstrate the sensitivity of the consumption estimates to the method for estimating diet composition.

Materials and methods

Diet composition models

If we could randomly select a sample of n prey items consumed by pinnipeds, a ratio estimator (Cochran, 1977) would be appropriate to estimate the proportion of biomass (π_i) represented by the i^{th} prey species from ω possible prey species:

$$\hat{\pi}_i = \frac{b_i}{\sum_{i=1}^{\omega} b_i} = \frac{n_i \overline{w}_i}{\sum_{i=1}^{\omega} n_i \overline{w}_i}, \quad (1)$$

where b_i = the total biomass of the n_i prey items that are species i;
$\overline{w}_i = b_i / n_i$ = the average mass for species i; and
$n = \sum_{i=1}^{\omega} n_i$.

Prey hard-parts in a scat represent a filtered selection of the prey species that were consumed by a single animal over some unknown and variable amount of time. Captive feeding studies have shown that a scat does not represent a single meal or even a single fixed period of feeding time (Harvey, 1989). Moreover, pinnipeds are unlikely to consume the same amount of prey in each meal or in a specified amount of time. Therefore, the biomass represented by the prey remains in a scat is unlikely to be constant because consumption varies. From a collection of s scats in which each scat represents a variable amount of biomass that is proportional to consumption, the ratio estimator (Eq. 1) is also appropriate, where b_i is the total biomass of species i from the s scats. We will refer to (Eq. 1) as biomass reconstruction (BR), which is equivalent to the estimator used by Harvey (1988) and Hammond and Rothery (1996).

Alternatively, one could argue that the biomass reconstructed from prey remains in a scat may vary for numerous reasons other than consumption. Variation in scat volume and production and the resulting amount of hard parts may be affected by factors that influence digestion and deposition (e.g. seal activity level). Also, it may not always be possible to collect an entire scat or even reasonably define a scat as a discrete entity. Thus, even though consumption by seals varies to some degree, the biomass reconstructed from a scat may vary much more than the variation in consumption. Thus, one could argue that each scat should be treated as a "representative" variable-size sample of a nearly constant amount of biomass consumed during some feeding interval. With that conceptual sampling model, the most appropriate estimator would be a simple average of the proportions in each scat:

$$\hat{\pi}_i = \frac{\sum_{k=1}^{s} \hat{\pi}_{ik}}{s} = \frac{\sum_{k=1}^{s} \left(\frac{b_{ik}}{\sum_{i=1}^{\omega} b_{ik}} \right)}{s} = \frac{\sum_{k=1}^{s} \left(\frac{n_{ik} \overline{w}_{ik}}{\sum_{i=1}^{\omega} n_{ik} \overline{w}_{ik}} \right)}{s} \quad (2)$$

where b_{ik} = the biomass of species i;
n_{ik} = the number of species i consumed; and
$\overline{w}_{ik}$ = the average mass of species i in the k^{th} scat.

Equation 2 is similar to the estimator of Olesiuk (1993), which he called split-sample frequency of occurrence (SSFO):

$$\hat{\pi}_i = \frac{\sum_{k=1}^{s} \left(\frac{I_{ik}}{\sum_{i=1}^{\omega} I_{ik}} \right)}{s}, \quad (3)$$

where I_{ik} = an indicator variable which equals 1 if one (or more) prey items of species i is in scat k, and 0 otherwise.

Equation 2 is equivalent to 3 when you make Olesiuk's (1993) assumption that an equal amount of biomass of each species in the scat was consumed. SSFO requires only a determination of the presence or absence of the prey in a scat, and thus, it is much easier to implement than either Equations 1 or 2, which require an enumeration of the individual prey in each scat and their mass.

Enumeration of prey in a scat sample is straightforward with unique structures such as otoliths. However, by using nonunique hard parts (e.g. gillrakers, vertebrae) to reduce selection bias resulting from unequal digestibility of otoliths, problems are introduced with enumeration. When prey are exclusively represented in scat by nonunique structures, it may be possible only to determine that a single individual was consumed or at best a minimum number can be constructed by enumerating nonunique structures and dividing by the average number of structures per fish (e.g. count of vertebrae divided by average number of vertebrae per fish). By including nonunique structures, enumeration of prey is replaced with an estimate of the

minimum number of prey ($\hat{n}_i$) consumed. For some hard parts, it may not be possible to identify the species, but the hard part can be classified to a group of species, such as family. In these cases, the species can be grouped into a single unit for estimation (e.g. all hexagrammids) or the unidentified prey can be partitioned to species based on the sample of species-specific hard parts. For example, most salmonid bones are currently indistinguishable to species; therefore salmonids in scats represented by bones (u) can be apportioned into species from proportions (γ_i) observed from otoliths (o_i). If we denote Ψ to be the set of all identified salmonids represented by otoliths, the number of salmonid prey in species i can be estimated as

$$\hat{n}_i = o_i + u\hat{\gamma}_i \quad \text{for } i \in \Psi. \tag{4}$$

where

$$\hat{\gamma}_i = \frac{o_i}{\sum_{i \in \Psi} o_i} \quad \text{for } i \in \Psi. \tag{5}$$

Prey mass can be determined from morphometric relationships between hard part dimensions (e.g. typically otolith length) and mass. Adjustments should be made to account for partial digestion of the hard part. From regressions between otolith length (corrected for degradation) and fish length and between fish length and mass, an estimate of the average mass of prey represented in scat can be constructed (Harvey et al., 2000; Browne et al., 2002). In some scats, a prey species may be represented only by hard parts (e.g. gillrakers) that do not have a quantifiable relationship to mass. We have to assume that the prey with unknown mass are represented by the average mass determined from the measurable hard parts (e.g. unbroken otoliths) of that species.

Thus, the biomass cannot strictly be measured but must be estimated by using estimated average mass ($\overline{w}_i$) and estimated number of individual prey ($\hat{n}_i$):

$$\hat{b}_i = \hat{n}_i \frac{\sum_{j=1}^{o_i^*} \hat{w}_{ij}}{o_i^*} = \hat{n}_i \overline{w}_i, \tag{6}$$

where o_i^* = the number of hard parts (typically unbroken otoliths); and
$\hat{w}_{ij}$ = the estimated mass derived from the regressions relating otolith length to fish mass.

To estimate number of prey consumed (P_i) rather than biomass, estimated biomass is divided by average mass:

$$\hat{P}_i = \frac{\hat{B}_i}{\overline{w}_i} = \xi \frac{\hat{\pi}_i}{\overline{w}_i} = \xi \hat{\rho}_i, \tag{7}$$

where $\hat{\rho}_i = \dfrac{\hat{n}_i}{\sum_{r=1}^{\omega} \hat{b}_r}$ = the number of prey species i consumed per unit of biomass consumed.

Pinniped diet can be quite variable in response to prey availability (Pierce et al., 1991; Tollit et al., 1997a; Browne et al., 2002; Beach et al.[1]; Brown et al.[2]). Because scat collected at a single date may reflect what was locally available at that time, collecting scats at different times throughout a season or year will provide a better representation of diet. From scats collected across several occasions, what is the best way to estimate average diet composition? If the amount of scat collected and resulting reconstructed biomass for an occasion is proportional to the amount of prey consumed, the data should be pooled for a single ratio estimate. However, in many cases the amount of scat collected will reflect a multitude of factors, such as tide height, storms, human disturbance, and the length of time that the seals were at the haulout prior to collection. Also, in many circumstances a fixed number of scats are collected rather than some fixed proportion of the scats available at the haulout. Therefore, we suggest that an average of the proportions (ratios) is appropriate. If there are T occasions, the average proportion is

$$\hat{\pi}_i = \frac{\sum_{t=1}^{T} \hat{\pi}_{it}}{T}. \tag{8}$$

Often there are seasonal shifts in diet resulting from prey availability (Olesiuk et al., 1990; Tollit and Thompson, 1996; Browne et al., 2002). In such cases, the analysis should be stratified by season. If data are collected over several years, again a simple average of the seasonal proportions is appropriate. In the appendix, we provide variance estimators for diet composition and consumption estimates for data collected over several years stratified by season.

Data collection and analysis

For the data used in this paper, Browne et al. (2002) have described the scat collection and analytical methods and have provided descriptions of the food habits from these data. As in Browne et al. (2002), we stratified our data collection and analysis into three seasons, spring (1 March–14 May), summer (15 May–15 July) and fall (16 July–15 October), based on the timing of chinook salmon runs at the Bonneville Dam, offset by two weeks to account for the travel of salmonids from the lower Columbia River to the Dam (at river km 235). We describe here additional meth-

[1] Beach, R. J., A. C. Geiger, S. J. Jefferies, S. D. Treacy, and B. L. Troutman. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC Processed Rep. 85-03, 316 p. Northwest and Alaska Fisheries Sci. Cent., Nat. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Brown, R. F., S. D. Riemer, and S. J. Jeffries. 1995. Food of pinnipeds collected during the Columbia River Area Commercial Salmon Gillnet Observation Program, 1991–1994. Wildlife Diversity Program Tech. Rep. 95-6-01, 16 p. Oregon Department of Fish and Wildlife, 2501 SW 1st Ave., PO Box 59, Portland, OR 92707.

ods for development of estimates of prey consumption by harbor seals.

Prey remains were usually identified to species, but in some cases could only be identified to genus, family, or larger taxon (e.g. flatfish). Our primary interest was salmonid consumption; therefore, where possible, we also classified salmonids as juvenile or adult. For non-salmonids, we were less interested in species-specific estimates of consumption; therefore we did not always identify nonotolith remains to species when identification was either time-consuming or uncertain. For example, we divided flatfish into starry flounder (*Platichthys stellatus*) and "other flatfish" because starry flounder were easily identified, but the remaining flatfish species were not easily distinguishable. In some cases, prey remains could be identified to species, but they occurred infrequently; therefore we grouped them by family (e.g. Hexagrammidae) or groups of families (e.g. Stichaeidae and Pholididae). We have used the term "prey group" to generically refer to our classification of prey remains into family (or more general taxon), species, or species and size.

Both species and size of salmonids could be determined from unbroken otoliths. For most salmonids, even broken otoliths were classified as adult or juvenile because of a very apparent discontinuity in otolith size between adults and juveniles. However, for coho salmon (*O. kisutch*) and cutthroat trout (*O. clarkii*), the size difference between juveniles and adults was less obvious; therefore we did not classify broken otoliths. We partitioned coho salmon and cutthroat trout broken otoliths into adults and juveniles according to the observed seasonal proportion of unbroken otoliths for each species. Salmonids represented exclusively by bone were not separated by species or size, but were apportioned according to seasonal average proportions measured from otoliths.

The lengths of all unbroken otoliths were measured to compute an average mass for most prey. We corrected the measured length for an average amount of degradation (Browne et al., 2002). For Pacific mackerel (*Scomber japonicus*), elasmobranchs (sharks and skates), lamprey (*Petromyzontid* spp.) and peamouth chub (*Mylocheilus caurinus*), size relationships were not available; therefore literature values of average mass were used (Browne et al., 2002). For many species, there were very few measurable otoliths for an individual collection date; therefore an average weight was computed across all collection dates within that particular season and applied to each collection date during that season. If there were 10 or fewer hard parts measured in each season, we used the average and variance of the predicted weights from the data pooled over the three seasons (i.e. we assumed no seasonal differences).

The amount of prey biomass (ξ) required to sustain the harbor seals in the Columbia River during a season is a function of seal abundance (N), the age and sex proportions (θ_a) and the sex- and age-specific daily biomass requirements of the seals (C_a), and the length of the season (D):

$$\xi = N \sum_a \theta_a C_a D. \tag{9}$$

We confined our analysis to nonpup (>6 months) seals because weaned pups comprise a small proportion of the seals in the Columbia River and they primarily consume soft-bodied prey or crustaceans (Pitcher, 1980; Riemer and Brown[3]) which could not be incorporated into our estimates of diet composition. The average number of seals was determined from aerial surveys that were flown over seal haulout sites. Pups and nonpups were counted from photographic slides or they were counted during flights over small haulout sites. Aerial surveys were flown on 10 occasions between March and July 1995, on 16 occasions between March and June 1996, and on 25 occasions between March and September 1997. In 1997, radio-tags and visual markers were attached to 26 seals (8 adult males, 10 adult females, and 8 subadults) to estimate the average proportion of nonpup seals that were hauled out during the surveys (f) with the techniques described by Huber et al. (2001). The correction factor was used for all of the counts to construct average seasonal abundance estimates. Abundance of nonpup seals in each season was estimated by

$$\hat{N}_j = \frac{\bar{c}_j}{f}, \tag{10}$$

where $\bar{c}_j$ = the average count of nonpup seals hauled out during season j.

Age (other than unmolted pups) and sex of seals cannot be determined from aerial surveys; therefore, estimating the sex and age structure would require capturing seals at different times throughout the year. Instead, we relied on a predicted sex and age structure based on life-history table data (Bigg, 1969; Pitcher and Calkins[4]), but rescaled the proportions to the nonpup portion of the population. We used the following sex and age structure for nonpup seals (θ_a): a=1, 23% subadult (1–4 yr); a=2, 35% adult males (>4 yr); a=3, 42% adult females (>4 yr). We assumed the following biomass requirements for the three groups: C_1= 1.89 kg/d , C_2= 2.37 kg/d, and C_3= 2.63 kg/d. We derived these values by averaging the age-specific daily biomass requirements given by Olesiuk (1993). We did not include any variability in our estimates of biomass requirements, nor did we include any uncertainty in the estimates of the population structure (θ_a). Therefore, variability in ξ only included variation in the population estimate.

[3] Riemer, S. D., and R. F. Brown. 1997. Prey of pinnipeds at selected sites in Oregon identified by scat (fecal) analysis, 1983–1996. Wildlife Diversity Program Tech. Rept. 97-6-02. 34 p. Oregon Department of Fish and Wildlife, 2501 SW 1st. Ave., PO Box 59, Portland, OR 92707.

[4] Pitcher, K. W., and D. G. Calkins. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Final Rep. to OCSEAP (Outer Continental Shelf Environmental Assessemnt Program), Dept. Interior, Bur. Land Manage., 72 p.

Table 1

Apportionment of unidentified salmonid remains based on proportions of identified salmonid remains as species i in season j (γ_{ij}).

		Proportions (γ_{ij})			Apportioned unidentified ($\gamma_{ij}u_j$)		
Species	Age class	Spring	Summer	Fall	Spring	Summer	Fall
Chinook	Adult	0.038	0.083	0.462	2.3	2.3	30.9
	Juvenile	0.538	0.389	0.077	31.8	10.9	5.2
Coho	Adult	0.051	0.292	0.231	3.0	8.2	15.5
	Juvenile	0.026	0.000	0.154	1.5	0.0	10.3
Cutthroat	Adult	0.144	0.049	0.000	8.5	1.4	0.0
	Juvenile	0.144	0.146	0.077	8.5	4.1	5.2
Sockeye	Adult	0.019	0.000	0.000	1.1	0.0	0.0
Steelhead	Adult	0.019	0.014	0.000	1.1	0.4	0.0
	Juvenile	0.019	0.028	0.000	1.1	0.8	0.0
Total (u_j)					59	28	67

Table 2

Average and coefficient of variation (in parentheses) of the count ($\bar{c}_j$) of hauled-out nonpup seals, estimated abundance (N_j) and prey biomass requirements (ξ_j) for each season.

Season	Avg. count	Abundance	Required biomass (t)
Spring (1 Mar–14 May)	1012 (0.11)	1659 (0.12)	296.34 (0.12)
Summer (15 May–15 July)	823 (0.07)	1349 (0.10)	193.65 (0.10)
Fall (16 July–15 Oct)	598 (0.15)	980 (0.16)	214.21 (0.16)

Results

Scats were collected on 31 occasions during March–October 1995–97 providing 1385 scats with identifiable prey remains (Browne et al., 2002). All seasons were sampled in each year except for the fall of 1995. Remains were identified from 5832 different prey which were assigned to ω=28 prey groups. We excluded the very minor unidentified component. Salmonids of unknown species and size represented by bone (154) were partitioned based on the observed seasonal proportions (Eqs. 4 and 5, Table 1).

During 16 of the flights in 1997, the proportion of the 26 radio-tagged seals hauled out was measured to construct a single average correction factor ($1/f$) of 1.64 (percent coefficient of variation (CV)=6.7%) to estimate seasonal abundance from the haulout counts (Table 2). Using the assumed age and sex structure and biomass requirements, we estimated that the seals in the Columbia River would consume 704 metric tons (t) of biomass during the 7.5 month period (Table 2).

From the 1385 scats, we reconstructed 1.15 t of biomass which was only 0.16% of the required biomass consumption. Because the number of scats and seals varied between seasons, the percentages varied from 0.077% in spring, 0.173% in summer, and 0.272% in fall. Using BR, we constructed diet composition estimates (Fig. 1) and seasonal consumption estimates (Fig. 2). Many of the estimates of salmonid consumption had exceedingly poor precision with the coefficient of variation exceeding 0.5 (Table 3). Using adult chinook salmon (*O. tshawytscha*) as an example, an examination of the variance components demonstrated that estimation of biomass (Table 4) was the predominant source of variance. Variance associated with biomass estimation includes variation in predicted weights and estimation of number of prey ($\hat{n}_i$) for salmonids. The latter accounted for one- to two-thirds of the total variance for salmonids depending on the species and size group. The use of genetics to obtain species identification of the unknown salmonids identified by bone would substantially improve the precision for salmonids.

Using BR to estimate diet composition, adult chinook salmon was the only salmonid that was consistently in the five most important prey items for each season based on percent of biomass (Fig. 1). Their importance was derived from their average mass which was the largest of all the prey. Adult chinook salmon and the other salmonids appeared much less important if the ranking was based on the number consumed (Fig. 2). Smaller prey items such as herring (*Clupeid spp.*), sculpin (*Leptocottus armatus*), lamprey (*Petromyzontid spp.*), smelt (*Osmeridae*) and

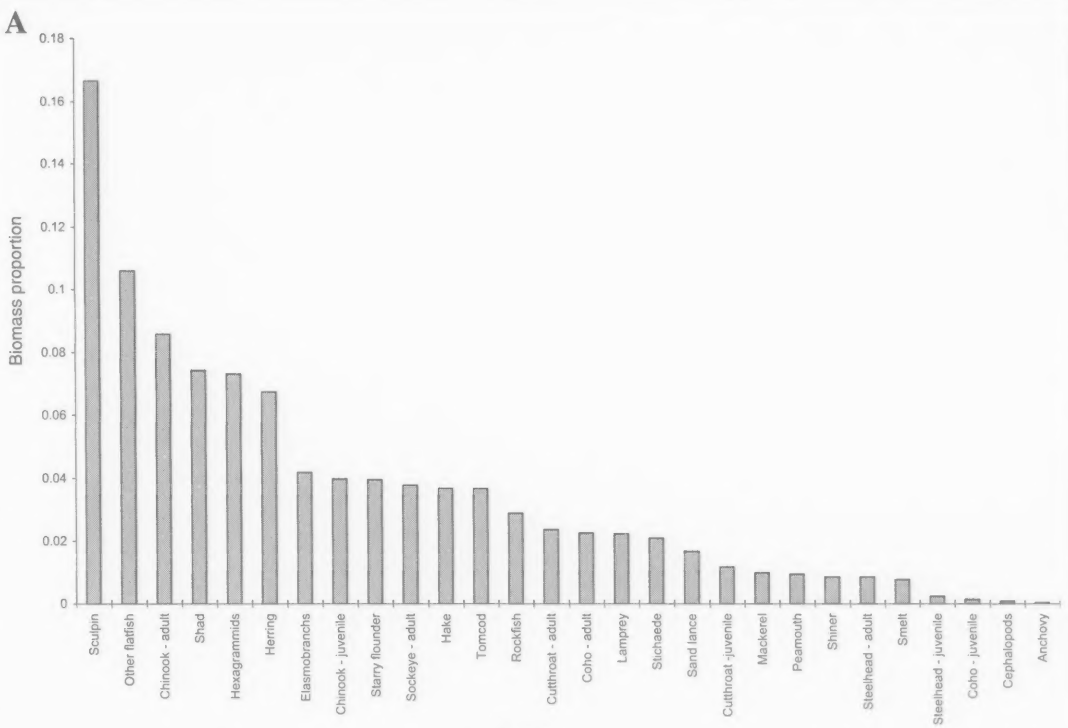

Figure 1

Average biomass proportion (π_j) of each prey group in the diet of harbor seals on the Columbia River between 1995 and 1997 for spring (**A**), summer (**B**), and fall (**C**).

Table 3

Average seasonal estimates of the number of salmonids consumed by harbor seals during 1995–97 (P_i) (in 1000s) and its coefficient of variation (CV) based on the biomass reconstruction (BR) method for diet composition.

		Spring		Summer		Fall	
Species	Size	P_i	CV	P_i	CV	P_i	CV
Chinook (*O. tshawytscha*)	Adult	3.9	0.65	3.1	0.44	15.6	0.30
	Juvenile	57.1	0.39	18.0	0.32	2.4	1.11
Coho (*O. kisutch*)	Adult	5.1	0.73	13.3	0.32	7.3	0.65
	Juvenile	2.8	0.85	0.0	0.00	4.9	0.76
Cutthroat (*O. clarkii*)	Adult	14.2	0.40	2.2	0.42	0.0	0.00
	Juvenile	14.2	0.40	6.6	0.38	2.3	1.08
Sockeye (*O. nerka*)	Adult	4.4	0.45	0.0	0.00	0.0	0.00
Steelhead (*O. mykiss*)	Adult	2.0	0.99	0.6	0.64	0.0	0.00
	Juvenile	2.0	1.00	1.3	0.57	0.0	0.00

anchovy (*Engraulis mordax*) were consumed in greater quantity but they were not always a large proportion of the reconstructed biomass.

Using split-sample frequency of occurrence (SSFO) to estimate diet composition, the results were dramatically different for larger and smaller prey items (Fig. 3). For

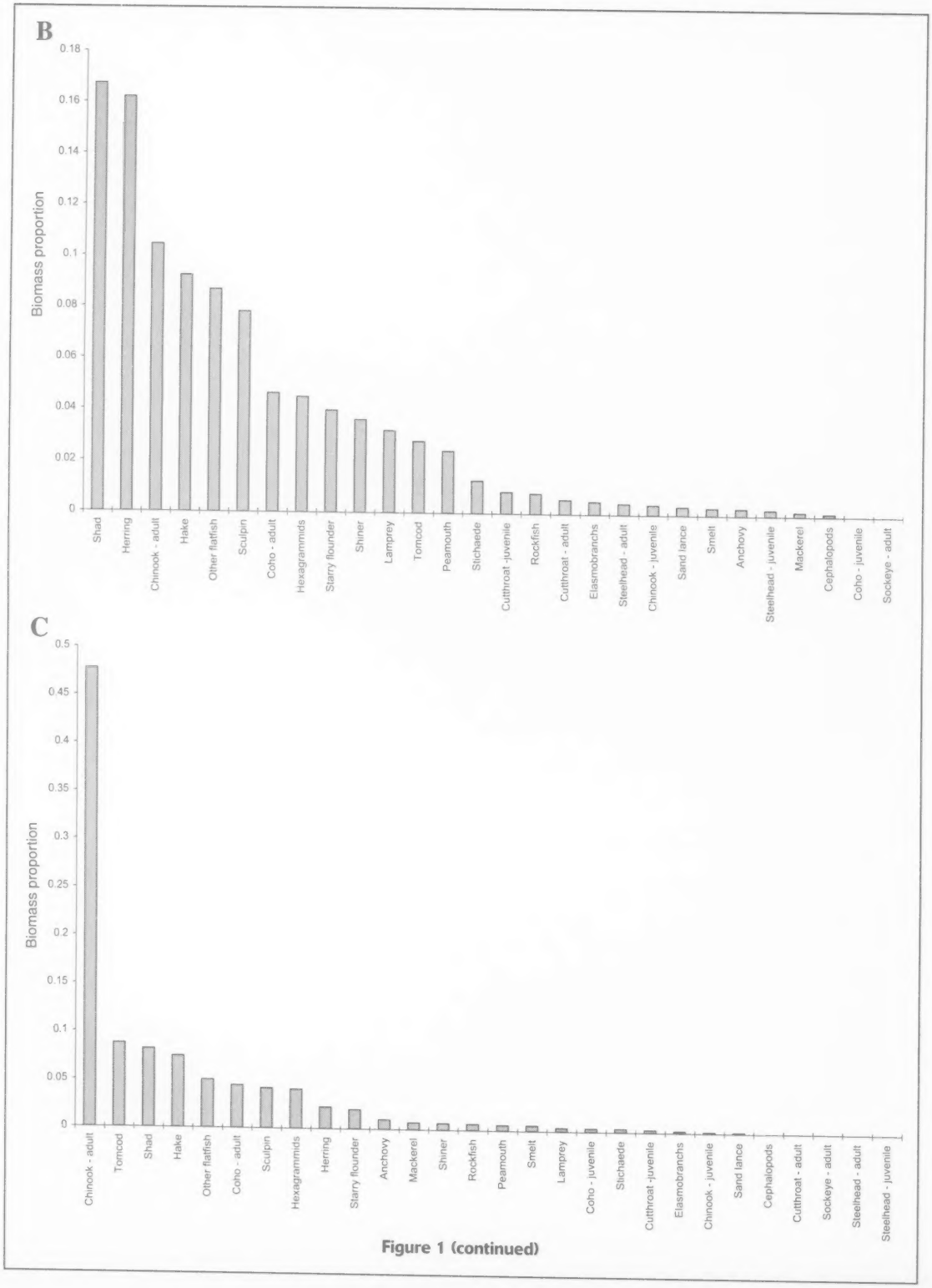

Figure 1 (continued)

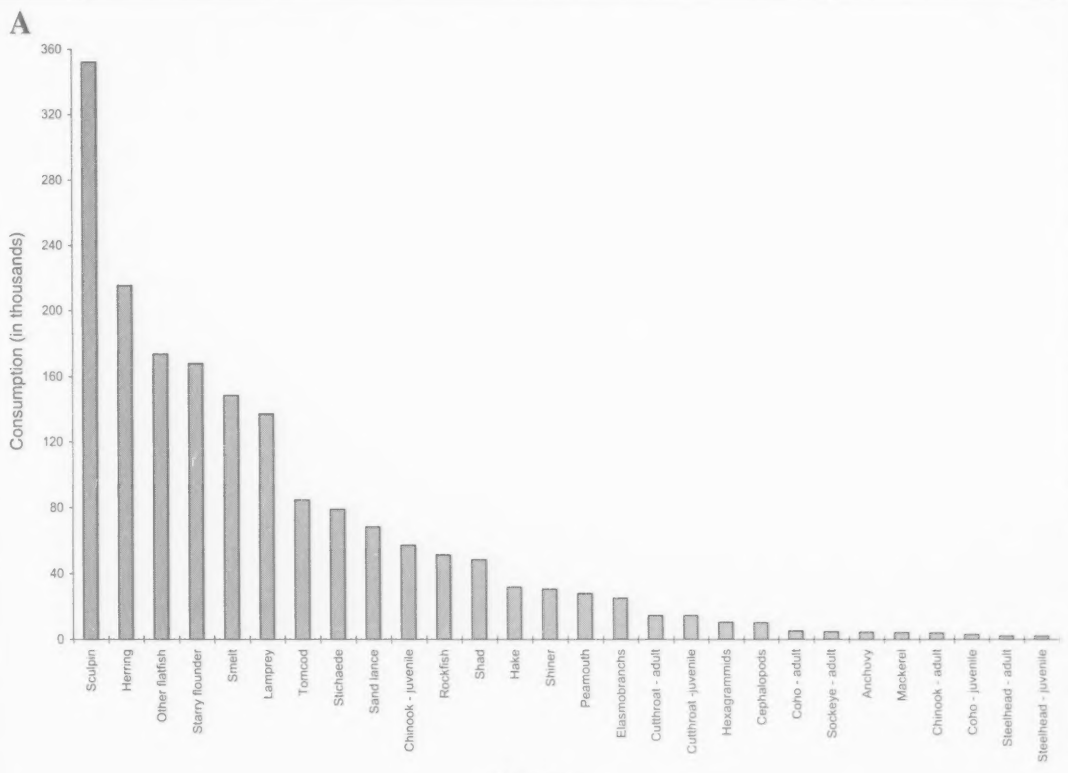

Figure 2

Estimates of the average consumption of each prey group (P_{ij}) by harbor seals on the Columbia River between 1995 and 1997 for spring (**A**), summer (**B**), and fall (**C**).

prey items weighing 10–20 g, SSFO predicted consumption that was 10 times greater than BR. Likewise, for prey items with a 1 kg mass or greater, SSFO predicted consumption estimates that were less than one-tenth of the BR estimate. For prey items near the median mass of 173 g, both estimators produced similar results.

Discussion

The consumption estimates for the Columbia River harbor seals could be improved by incorporating differences in energy density across prey and by measuring the sex- and age-structure of the seal population through time rather than using a life-table which may not be appropriate. These are valid criticisms and they could be overcome by collecting additional data. However, we believe these are less important than the current inadequacies in measuring diet composition that will likely affect any study that attempts to estimate consumption based on scat analysis.

It is well recognized that digestion does not act equally on all hard parts and is certainly species-specific for otoliths (Harvey, 1989). We included other hard parts such as bone to reduce bias due to differential otolith digestion; however, that inclusion may not remove all of the selectivity bias and it certainly introduces several other problems discussed below. Also, because hard parts are used for diet composition, if seals are only eating the fleshy parts of large fish, a significant portion of their diet may be missed.

Table 4

Proportion of variance of the adult chinook consumption estimate resulting from each estimation component.

	Diet composition		Harbor seal	
Season	Year (σ_y)	Date (σ_t)	Biomass (σ_r)	Population size
Spring	0.00	0.14	0.82	0.04
Summer	0.00	0.51	0.44	0.04
Fall	0.20	0.16	0.59	0.05

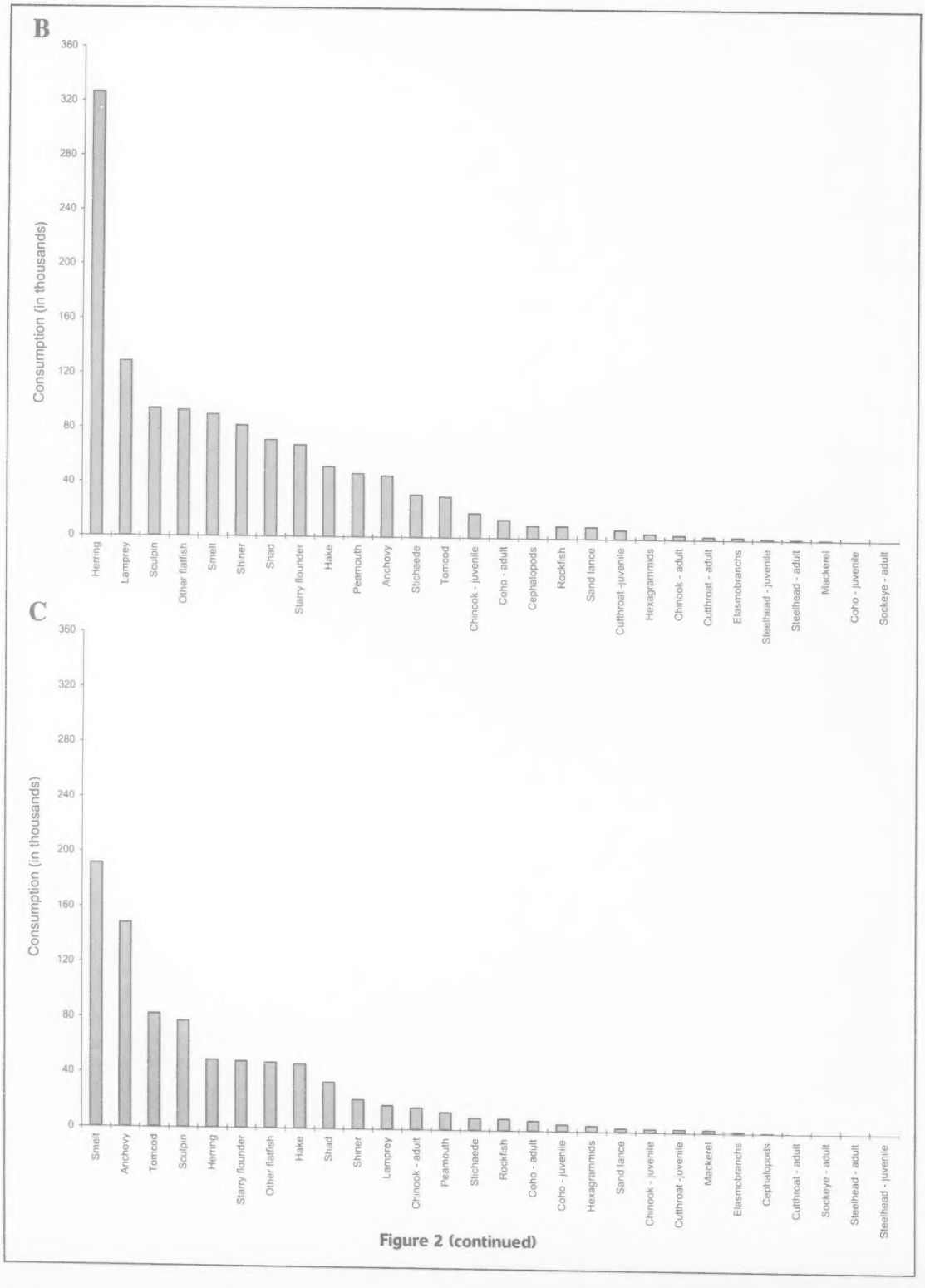

Figure 2 (continued)

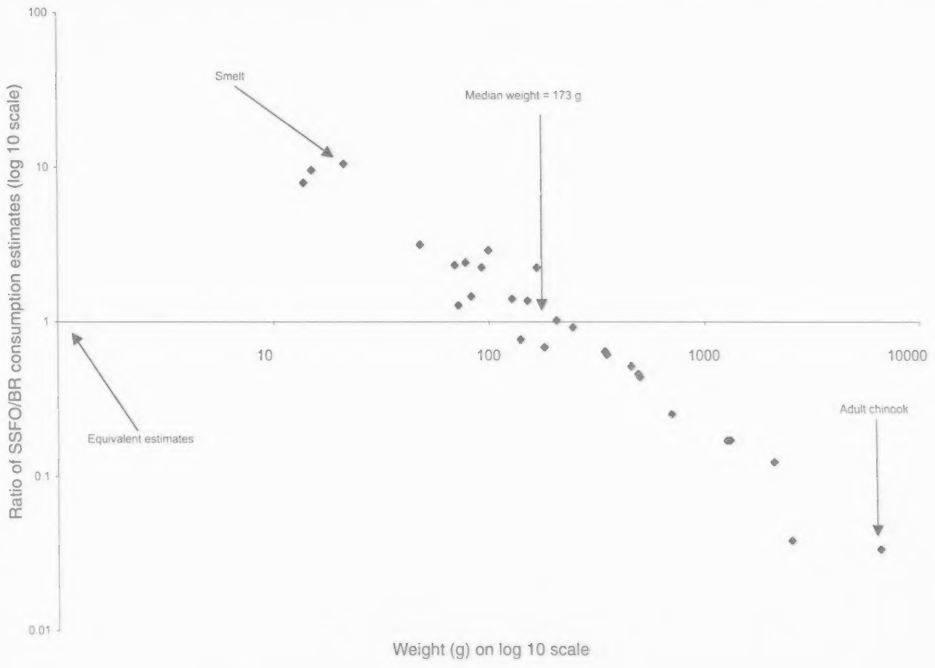

Figure 3

Comparison of spring consumption estimates for harbor seals on the Columbia River based on split-sample frequency of occurrence (SSFO) and biomass reconstruction (BR) in relation to prey weight. Similar estimates were obtained for prey near the median weight. SSFO increases estimates of smaller prey items (e.g. smelt) and decreases estimates of larger prey items (e.g. adult chinook salmon) in relation to BR.

We have assumed an equal probability of recovering identifiable skeletal remains from all prey sizes and that masses predicted from otolith measurements represent prey identified from other structures. There are several situations when recovered otoliths may not correctly represent the size of prey consumed. Small otoliths from small individuals of a species may be more likely to be completely digested. In that case, biomass would be overestimated because the larger otoliths would be recovered from larger fish. Also, otoliths may have different passage rates due to changes in their structure as fish age resulting in a size bias. Consumption estimates could thus be erroneously high or low because prey would be calculated from a single size group rather than the range of prey consumed. Unequal digestion may also create errors in estimated mass from the otoliths that are recovered. Our estimated mass may have been biased because we applied an average degradation factor to adjust otolith length. A better alternative would be to grade otolith condition and apply condition-specific degradation factors (Tollit et al., 1997b).

Counting the number of individual prey items is not possible with nonunique bones. Instead, we estimated a minimum number of individuals (MNI) contained in the scat (n_{ij}=MNI). MNI from all skeletal elements is a minimum estimate because the presence of many nonunique structures are assigned to a single prey item when they could represent several different prey. This error would not bias diet composition if it did not vary over species and size. However, differential passage of unique structures and identifiability among species result in the greater probability of detecting some prey (Browne et al., 2002). To minimize interspecific biases, we could use an MNI of 1 for all bones, regardless of the enumeration of unique structures for some species. While this would reduce some problems with species differences, it would exacerbate differences associated with prey size because large prey would be accurately reflected by an MNI of 1 and small prey that are eaten in greater quantities would be severely underestimated.

Bowen (2000) proposed estimating the number of prey consumed by correcting the otolith count with rates of otolith recovery from feeding trials. These correction factors vary widely between seals and studies and are influenced by a variety of factors, including size of individual prey, meal size, and activity of harbor seals (Harvey, 1989; Harvey and Antonelis, 1994; Cottrell et al., 1996; Tollit et al., 1997b). Browne et al. (2002) examined the ratio of otolith-

corrected estimates of MNI for several species. The ratios were quite variable but the comparison did suggest that smaller prey such as smelt were more likely to be underrepresented by using the minimum count.

If diet composition is based on sagittal otoliths, a fish can be represented by, at most, two scats and because all fish have two sagittal otoliths, fish size should not influence the probability that a particular fish is included, in a sample of scats, except through size-specific passage rates of otoliths. However, when all hard parts are included, the sampling may be size-biased if the size of the prey affects the number of scats in which the hard parts are deposited. Larger prey contain larger hard parts that may require longer passage times; therefore larger prey may be deposited in more scats than smaller prey. Also, large prey may be shared among seals as a result of cooperative feeding behavior and could be deposited in several scats. If either situation occurs, larger prey would be more likely to be included in the sample and would be over-represented. Because the scat is the sampling unit, any prey-size or species-specific effects on scat deposition rate may also bias diet composition estimators.

The effect of over-representing large prey depends on the estimator used for diet composition. The different outcomes with Equations 1–3 can be demonstrated with a simple example. Consider a sample of two scats in which one scat contains the remains of a 2-kg salmon and another scat contains the remains of ten 10-g anchovy and four 100-g herring. From Equation 1, the diet composition would be 80% (2000/2500) salmon, 4% anchovy, and 16% herring based on proportions of total reconstructed biomass. From Equation 2, we would estimate that salmon represent 50% of the diet from the two samples that are 100% and 0% salmon, and likewise 10% anchovy and 40% herring. Finally from Equation 3, we would estimate that the diet was 50% salmon, 25% anchovy, and 25% herring. If the small prey were undercounted in relation to the large salmon, the influence of the error influences the composition within the scat for Equations 2 and 3, but for BR (Eq. 1) the error extends across all samples.

As with the Columbia River harbor seal example (Fig. 3), the differences in the estimators are primarily the result of large prey in the weighted versus unweighted averages. Some difference would be expected in the results of Equations 2 and 3 depending on the validity of the equal volume assumption. SSFO (Eq. 3) simplifies the analysis of diet composition to a measure of presence and absence by assuming that prey within the same scat were consumed in equal volumes. The simplifying assumption removes the necessity to enumerate prey and measure mass from morphometric relationships with prey remains. However, the equal volume assumption does not seem particularly reasonable and its implementation is arbitrary, depending on how the prey are classified unless all prey remains can be identified to species. Olesiuk (1993) showed that the diet composition percentages for the primary prey varied by a factor of two or three, depending on the assumed composition within each scat. We expected that these differences would depend on the diversity of the diet. How closely they represented the true diet would depend on the range in prey sizes.

From our viewpoint, we do not see a clear choice between the estimators for diet composition. The use of consumption estimates from SSFO and BR to provide a range of estimates may have limited application in cases where each approach would suggest a similar conclusion. However, for large prey, such as salmonids, a tenfold difference in estimates, compounded with the uncertainty from sampling and biomass estimation, may yield too little information to develop a reliable conclusion about the impact of pinniped predation on salmonid stocks.

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Appendix

We have constructed variance estimators for diet composition and consumption rates using finite population sampling methods (Cochran, 1977) and delta method approximations based on the Taylor series (Seber, 1973). Variance estimates and confidence intervals could also be constructed by using bootstrap techniques similar to the work of Hammond and Rothery (1996).

To describe the variance estimators, we use the following subscripts: i for prey group, j for season, y for year, and t for collection occasion within year. A dropped subscript implies summation or averaging over that subscript (e.g. s_{jy} is the total number of scats collected in season j of year y—summed over occasions). We define the following notation which was not used in our article:

T_{jy} = number of scat collection occasions,
s_{jy} = number of scats collected during the occasion,
Y_j = number of years in which season j was sampled of a total of Y years.

We have assumed that scat collected on each occasion is a varying proportion of a fixed and unspecified amount of prey biomass consumed. Thus, we computed unweighted averages of the proportions over occasions and then over years:

$$\hat{\pi}_{ijy} = \frac{\sum_{t=1}^{T_{jy}} \hat{\pi}_{ijyt}}{T_{jy}} \quad \hat{\pi}_{ij} = \frac{\sum_{y=1}^{Y_j} \hat{\pi}_{ijy}}{Y_j}.$$

We have also assumed that scat samples are independent which would be a concern in the unlikely event that the same seal deposited multiple scats at one time. We have also assumed that the collection occasions which are limited to low tides represent a random sample of dates within a season.

The variance of diet composition was based on multistage sampling scheme stratified by season (Cochran, 1977) that was composed of the following stages: estimation of biomass proportion consumed for each occasion, sampling of occasions within season of a year, and sampling of years. We have limited inference to the Y years that were sampled. Thus, if a season was sampled in each

year there is no annual variance component. The variance of the diet composition for a prey group for a single season is the sum of three components corresponding to the three stages: estimation of biomass proportion (σ_b^2), sampling of occasions (σ_t^2), and sampling of years (σ_y^2). Following Cochran (1977), the estimators for each component are

$$\hat{\sigma}_b^2 = \frac{\sum_{y=1}^{Y_j}\sum_{t=1}^{T_{jy}} \widehat{Var}_b(\hat{\pi}_{ijyt})}{\sum_{y=1}^{Y_j} T_{jy}},$$

$$\hat{\sigma}_t^2 = \frac{Y_j}{Y}\frac{\sum_{y=1}^{Y_j}\sum_{t=1}^{T_{jy}}(\hat{\pi}_{ijyt}-\hat{\pi}_{ijy})^2}{\sum_{y=1}^{Y_j} T_{jy}\sum_{y=1}^{Y_j}(T_{yj}-1)},$$

$$\hat{\sigma}_y^2 = \frac{\left(1-\frac{Y_j}{Y}\right)\sum_{y=1}^{Y_j}(\hat{\pi}_{ijy}-\hat{\pi}_{ij})^2}{Y_j(Y_j-1)}.$$

We used the delta-method (Taylor series approximation) (Seber 1973) to estimate the variance of the estimated proportion for occasion t which expressed in matrix notation is

$$\widehat{Var}_b(\hat{\pi}_{ijyt}) = \widehat{Var}_b\left(\frac{\hat{b}_{ijyt}}{\sum_{r=1}^{\omega}\hat{b}_{rjyt}}\right) = \beta'\Sigma\beta,$$

where β is a vector of partial-derivatives of π_{ijyt} with respect to b_{rjyt} for r=1, ω and Σ is the $\omega \times \omega$ variance-covariance matrix of b_{rjyt} for r=1,ω. Likewise, the variance of ρ_{ij} was estimated by using

$$\widehat{Var}(\hat{\rho}_{ij}) = \left[\frac{\hat{\sigma}_y}{\overline{w}_{ij}}\right]^2 + \left[\frac{\hat{\sigma}_t}{\overline{w}_{ij}}\right]^2 + \hat{\sigma}_\rho^2,$$

where $$\hat{\sigma}_\rho^2 = \frac{\sum_{y=1}^{Y_j}\sum_{t=1}^{T_{jy}} \widehat{Var}_b(\hat{\rho}_{ijyt})}{\sum_{y=1}^{Y_j} T_{jy}},$$

and $$\widehat{Var}_b(\hat{\rho}_{ijyt}) = \widehat{Var}_b\left(\frac{\hat{n}_{ijyt}}{\sum_{r=1}^{\omega}\hat{b}_{rjyt}}\right) \approx \beta'\Sigma\beta,$$

where the elements in Σ and β for the i^{th} prey group are partitioned into $\hat{n}_{ijyt}$ and $\overline{w}_{ij}$. We also used the delta-method to obtain approximate variances and covariances in Σ of the biomass estimates for a single occasion

$$\widehat{Var}(\hat{b}_{ijyt}) = \hat{n}_{ijyt}^2\hat{\sigma}_{\overline{w}}^2 + \hat{\sigma}_{\hat{n}}^2\overline{w}_{ij}^2.$$

The first term in the variance is the uncertainty resulting from the variability in the estimate of the mean weight. For salmonid species, the second term measures the uncertainty resulting from apportioning the number of unknown salmonids into prey groups (i.e. estimating n_{ijyt}). For nonsalmonid species, all hard parts were classified into less specific prey groups; therefore $\hat{\sigma}_{\hat{n}} = 0$. The group-specific estimates of biomass within season are uncorrelated except for the estimates for salmonid species ($i\varepsilon\Psi$) which are correlated because of the apportionment of the items which were identified as salmonid but could not be identified to species nor to the juvenile and adult sizes. For salmonid groups r and $v\varepsilon\Psi$, the estimated covariance is

$$\widehat{Cov}(\hat{b}_{rjyt}\hat{b}_{vjyt}) = \widehat{Cov}(\hat{n}_{rjyt},\hat{n}_{vjyt})\overline{w}_{rj}\overline{w}_{vj}.$$

The total amount of biomass represented by the scats is the sum across all prey groups:

$$\hat{b}_{jyt} = \sum_{i=1}^{\omega}\hat{b}_{ijyt},$$

and its variance was estimated as

$$\widehat{Var}(\hat{b}_{jyt}) = \sum_{i=1}^{\omega}\widehat{var}(\hat{b}_{ijyt}) + 2\sum_{r\varepsilon\Psi}\sum_{v>r\varepsilon\Psi}\widehat{cov}(\hat{b}_{rjyt},\hat{b}_{vjyt}).$$

The variance of n_{ijyt} was estimated assuming a binomial distribution:

$$\widehat{Var}(\hat{n}_{ijyt}) = \sigma_{\hat{n}}^2 = u_{jyt}^2\frac{\hat{\gamma}_{ij}(1-\hat{\gamma}_{ij})}{o_{ij}},$$

and the covariance between salmonid groups was estimated as

$$\widehat{Cov}(\hat{n}_{rjyt},\hat{n}_{vjyt}) = -u_{iyt}^2\frac{\hat{\gamma}_{rj}\hat{\gamma}_{vj}}{o_{ij}}.$$

We assumed that the weights of the prey consumed were independent samples from a group- and season-specific distribution with mean μ_{ij}, and variance σ_{ij}^2. The parameters μ_{ij} and σ_{ij}^2 were estimated with the predicted weights from the sample of o^*_{ij} measurable hard parts:

$$\hat{\mu}_{ij} = \overline{w}_{ij} = \frac{\sum_{u=1}^{o^*_{ij}}\hat{w}_{iju}}{o^*_{ij}} \quad \text{and} \quad \hat{\sigma}_{ij}^2 = \frac{\sum_{u=1}^{o^*_{ij}}(\hat{w}_{iju}-\overline{w}_{ij})^2}{o^*_{ij}-1}.$$

To incorporate uncertainty in regression parameters and prediction error for the measured hard parts and variability in mass for the unmeasured prey ($n_{ij} - o^*_{ij}$), the variance of μ_{ij} should be estimated by

$$\widehat{Var}(\overline{w}_{ij}) = \hat{\sigma}^2_{\overline{w}} = \frac{\sum_{u=1}^{o^*_{ij}} \widehat{Var}(\hat{w}_{iju})}{o^{*2}_{ij}} + \left(\frac{n_{ij} - o^*_{ij}}{n_{ij}}\right)\frac{\hat{\sigma}^2_{ij}}{o^*_{ij}},$$

where the variance of $\hat{w}_{iju}$ is the prediction variance for the u^{th} otolith. When these data were analyzed, the available regression equations in a draft version of Harvey et al. (2000) did not include standard errors for the parameters nor the residual variance that were needed to compute the prediction variance. Therefore, unfortunately we had to drop the first term from the variance. The necessary values are now available in Harvey et al. (2000). The second-term measures variability between prey and is typically larger than the prediction error. However, to avoid underestimating this component of variance we dropped the finite population correction (fpc) factor on the second term. If we had used the fpc for salmonids, we would have had to replace the unknown n_{ij} with their estimated values.

For variance estimates of number of prey consumed (P_{ij}) we also used a delta method approximation:

$$\widehat{Var}(\hat{P}_{ij}) \approx \hat{P}^2_{ij}\left[cv^2(\xi_j) + cv^2(\hat{\rho}_{ij})\right].$$

We did not have variance estimates for energetic requirements nor age structure; therefore the variation in estimated prey biomass requirement (ξ_j) reflected only variation in our estimates of population size:

$$cv(\xi_j) = cv(\hat{N}_j) \approx \sqrt{cv^2(\bar{c}_j) + cv^2(f)},$$

which was also approximated by the delta method.

Abstract—The vertical and horizontal movements of southern bluefin tuna (SBT), *Thunnus maccoyii*, in the Great Australian Bight were investigated by ultrasonic telemetry. Between 1992 and 1994, sixteen tuna were tracked for up to 49 h with depth or combined temperature-depth transmitting tags. The average swimming speeds (measured over the ground) over entire tracks ranged from 0.5 to 1.4 m/s or 0.5 to 1.4 body lengths/s. The highest sustained swimming speed recorded was 2.5 m/s for 18 hours. Horizontal movements were often associated with topographical features such as lumps, reefs, islands and the shelf break. They spent long periods of time at the surface during the day (nearly 30%), which would facilitate abundance estimation by aerial survey. At night, they tended to remain just below the surface, but many remained in the upper 10 m throughout the night. SBT were often observed at the thermocline interface or at the surface while travelling. A characteristic feature of many tracks was sudden dives before dawn and after sunset during twilight, followed by a gradual return to their original depth. It is suggested that this is a behavior evolved to locate the scattering layer and its associated prey when SBT are in waters of sufficient depth. SBT maintained a difference between stomach and ambient temperature of up to 9°C.

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Vertical and horizontal movements of southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight observed with ultrasonic telemetry

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Southern bluefin tuna, *Thunnus maccoyii*, spawn in the northeast Indian Ocean south of the Sunda Islands from August to May (Farley and Davis, 1998). Young-of-the-year move down the west coast of Australia and first appear in the Great Australian Bight as 1-year olds. They aggregate in the Bight during the Austral summer, disperse to the east or west within latitudes of 30–40°S in autumn, and return to the Bight in spring. Juveniles between 1 and 4 years old return each summer to the Bight where they form extensive surface schools.

To provide a fishery-independent index of recruitment, line transect aerial surveys have been flown in the Bight each summer since 1990 to estimate the relative abundance of juveniles visible in the top 5 m (Chen et al.[1]). The largest source of variance in these estimates is thought to be environmental factors that influence both surfacing behavior and aerial detection. To investigate these problems, we used ultrasonic telemetry to provide the first information on surfacing behavior and short-term horizontal and vertical movement patterns that might influence sightings from the air. More comprehensive information on tuna surfacing for the whole of the three-month survey period is expected from an archival tagging program begun in 1992 (Gunn et al.[2]). Because these data are dependent upon the recapture of archival-tagged fish, this information will not be available for some time.

Because of Carey's pioneering work on Atlantic bluefin tuna (Carey and Lawson, 1973), ultrasonic telemetry has been used to study many tuna species, including Atlantic (Lutcavage et al., 2000) and Pacific bluefin tuna (Marcinek et al., 2001), yellowfin tuna (Carey and Olsen, 1982; Cayré and Chabanne, 1986; Yonemori, 1982; Holland et al., 1990a; Cayré, 1991; Cayré and Marsac, 1993; Block et al., 1997; Brill et al., 1999; Marsac et al.[3]), skipjack tuna (Yuen, 1970; Dizon et al., 1978; Levenez, 1982; Cayré and Chabanne, 1986; Cayré, 1991), bigeye tuna (Holland et al., 1990a, 1992; Holland and Sibert, 1994), and albacore (Laurs et al., 1977). A number of small (35–46 cm) southern bluefin tuna (SBT) have been tracked in the Indian Ocean off

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Western Australia (Fishery Agency of Japan[4,5]). All SBT in the current study were released and tracked in shelf waters, except for one fish that moved from the shelf into slope waters.

Methods

Tracking experiments on SBT were carried out in the Great Australian Bight over three years. In 1992, the tracking system was tested on a short cruise late in the fishing season and close to Port Lincoln. In 1993, the strategy was to obtain extended tracks of up to 48 hours to investigate day and night patterns in depth distribution and horizontal movement within the Great Australian Bight. In 1994, we planned short tracks to maximize the number of individual fish observed during daytime, so that their behavior could be linked to sightings by aerial survey carried out at the same time.

All SBT were caught by pole and line, except for tuna no. 7 (referred to simply as "tuna 7") which was caught on light game fishing tackle, and tuna 9, which swallowed the tag while free-swimming. The tuna were landed on a wet, plastic-covered, foam mat. The head was covered with a wet cloth, length of fish was measured, the tag attached or inserted, and the fish was released back into the school.

V16 (16 mm diameter) sonic tags (VEMCO, Halifax, Nova Scotia, Canada) of various frequencies (50–69 kHz), equipped with pressure sensors, were deployed on two fish in April 1992 and four fish in January and March 1993 (Table 1). Five of these tags were attached externally, behind the second dorsal fin of the tuna, by using the attachment technique described in Holland et al. (1985). The sixth was placed in the stomach with an oesophageal catheter.

V22 (22 mm diameter) tags transmitting on 40 kHz were used on ten tuna tracked in January and February 1994. These tags, which have stronger signals and lower transmission frequencies, have a much larger detection range than V16 tags. They also have the capacity for

Table 1
Release and tracking details of southern bluefin tuna tracked in the Great Australian Bight during the years 1992–94.

Tuna no.	Tag type	Date of release	Location	Length (cm)	Tag position	Duration of track (h)	Distance moved (km)	Mean speed		Cause of termination
								m/s	FL/s	
1	V16-P	29 Apr 1992	Cabbage Patch	90	external	12	34	0.79	0.87	weather
2	V16-P	30 Apr 1992	Cabbage Patch	90	external	18	48	0.74	0.83	poor signal
3	V16-P	27 Jan 1993	28 km W of Ward Island	94	external	49	175	0.99	1.06	voluntary
4	V16-P	30 Jan 1993	Ward Island	96	external	48	143	0.83	0.86	voluntary
5	V16-P	13 Mar 1993	Rocky Island	103	external	5	9	0.52	0.51	lost
6	V16-P	14 Mar 1993	Rocky Island	98	stomach	26	131	1.40	1.42	weather
7	V22-P	10 Jan 1994	7 km S of Cannan Reef	67	stomach	30	91	0.84	1.26	voluntary
8	V22-P	12 Jan 1994	7 km S of Cannan Reef	100	stomach	10	32	0.90	0.90	voluntary
9	V22-P	15 Jan 1994	Nuyts Reef	85	mouth	5	15	0.85	1.00	tag detached
10	V22-PT	16 Jan 1994	11 km SE of St Francis Island	92	stomach	13	40	0.85	0.93	tag regurgitated
11	V22-PT	17 Jan 1994	41 km W of Sceale Bay	114	stomach	13	46	0.98	0.86	tag regurgitated
12	V22-P	18 Jan 1994	41 km W of Sceale Bay	85	stomach	13	34	0.72	0.85	voluntary
13	V22-PT	19 Jan 1994	15 km W of Labatt Pt.	100	stomach	20	67	0.94	0.94	voluntary
14	V22-P	31 Jan 1994	41 km E of Sceale Bay	100	stomach	9	36	1.10	1.10	voluntary
15	V22-P	1 Feb 1994	7km S of Cannan Reef	102	stomach	1	2	0.64	0.63	fish lost
16	V22-P	2 Feb 1994	7km S of Cannan Reef	97	stomach	5	14	0.79	0.82	tag regurgitated

[4] Fishery Agency of Japan. 1990. Report of 1988 research cruise of the R/V *Shoyo-Maru*. Distribution of juvenile southern bluefin tuna off west coast of Australia, December 1988–January 1989. Rep. Res. Dep., Fish. Agency Jpn. 63:1–125. Pelagic Fish Resource Division, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

[5] Fishery Agency of Japan. 1992. Report of 1989 research cruise of the R/V *Shoyo-Maru*. Distribution of juvenile southern bluefin tuna off west coast of Australia, September–December 1989. Rep. Res. Dep., Fish. Agency Jpn. 64:1–166. Pelagic Fish Resource Division, 5-7-1 Orido, Shimizu, Shizuoka 424, Japan.

dual channels enabling sequential transmission of pressure and temperature. Seven pressure tags and three pressure-temperature tags were deployed. All, except one, were inserted into the stomach. To retard regurgitation, two small hooks were tied to each tag with VICRYL dissolving sutures before being placed in the stomach. One tuna struck a tag with hooks during a calibration experiment, resulting in the tag attaching without the tuna leaving the water. This fish was tracked for five hours until the tag detached.

Standard tracking techniques were used (see Holland et al., 1985). The tracking equipment, including the remote-controlled hydrophone rotator, is described in Pepperell and Davis (1999). We attempted to track the fish at a distance of about 400 m, which we judged from signal strength, using distance and signal-strength calibrations carried out before tracking. The decoded data from single-channel tags were logged together with global positioning system (GPS) latitude and longitude, nominally at 1-second intervals, on a computer with VEMCO VSCAN/GPS software (Vemco, 1992). Temperature and depth data from dual-channel transmitters were logged at about 3-second intervals.

Conductivity-temperature-depth profiles were taken at the start and finish, and at convenient times during each track, with a digital data loggers international profiler. Additional information collected during each track included bottom depth, air temperature, wind speed, cloud cover (1–8 sectors covered), brightness (1–4), and presence of surface and subsurface schools of SBT. In 1994, we also recorded the depth distributions of SBT schools detected on the echosounder under the tracking vessel.

The tracking data were processed using a filtering program to delete spurious data, interpolate missing data, and generate data files at nominated time intervals. The program compared each depth with the seven previous data points (which were nominally recorded at 1-second and 3-second intervals for single- and dual-channel tags, respectively) and then deleted spurious records based on expected maximum and minimum depths and maximum depth-change rates. Similarly, a temperature filter deleted spurious values based on expected maximum and minimum temperatures and maximum temperature-change rates in data from the dual-channel transmitters. Complete vertical tracks were plotted against time with 20-second interval data. The position and sustained swimming speeds of tracked tuna were assumed to be the same as that of the tracking vessel. By using GPS data, speed was calculated over the ground from the straight-line distance travelled between points in 10 minutes. Vertical movements and horizontal movements in relation to the vessel were not considered. An attempt was made to match both the heading and speed of the tracked tuna so that the vessel reflected the movements of the fish.

Depth distribution of tuna was examined from 20-second interval data aggregated in 5-m depth bins stratified by day and night. The number of observations in each depth bin was then expressed as a proportion of the total number of observations in each day–night stratum. The speed distribution of tuna was examined from 10-minute interval data aggregated in 0.1 m/s bins stratified by day and night.

Results

The tracking system was developed for use on a variety of commercial vessels. In April–May 1992, five fish were released and two were tracked successfully (Table 1). Modifications were then made to the system and different transmission frequencies were selected to reduce interference. The improved system was used on two cruises in January and March 1993. Four fish were tracked for periods of up to 49 h (Table 1).

In 1994, tracking was carried out farther west because fish schools were not sighted farther east (Fig. 1), probably due to warm water remaining in the northwest section of the study area (Fig. 2). The whole period (8 January–3 February) was characterized by windy conditions that made catching and tracking fish difficult. Ten SBT were released with tags (Table 1). The longest track was 31 h, but some tracks were short because the fish regurgitated their tags. Other tracks were terminated voluntarily after sunset to maximize the number of daytime observations on different fish.

Tuna 1 was released SW of Liguana Island on 29 April 1992 at 0855 h (Figs. 1 and 2A). It headed WSW towards the shelf edge until tracking was terminated after 12 hours. Acoustic interference from the tracking vessel affected calculation of depth at certain vessel speeds, resulting in some gaps in the vertical data (Fig. 3A). During the day the fish spent most of its time at the surface, but frequently dived to near the bottom. Tuna schools spotted at the surface appeared to break up and then re-appear sometime later, more or less at the same rate that the tracked SBT moved in and out of the surface waters. The fish dived shortly after sunset and then returned to the mixed layer and oscillated around 30 m until tracking was terminated at 2108 h.

Tuna 2 was released SW of Liguana Island on 30 April 1992 at 1330 h (Fig. 1). The fish moved west throughout most of the track but slowed and changed direction many times from 0400 h. These direction changes occurred when the tuna reached cooler surface waters (Fig. 2A). It remained in the 17°C water, moving south along the boundary with the 16°C isotherm. Its vertical behavior can be seen in Figure 3B. Like tuna 1, this fish made a brief dive just after sunset.

Tuna 3 was released at The Lump, 28 km west of Ward Island on 27 January 1993 at 15:22 h and was tracked for 49 h (Figs. 1 and 2B). It moved into waters near the shelf edge, a movement matched by a conventionally tagged tuna that was released at 33°15′S, 133°49′E on 26 January 1993 and that was recovered five days later at 34°S, 132°17′E by a commercial fishing operation. The vertical behavior of tuna 3 is shown in Figure 4A. It spent considerable time near the surface in association with other tuna during the late afternoon on the first day. It seldom surfaced on the second day; neither did the other tuna. A commercial pole-and-line boat fishing in the same area

Figure 1

Geographic position of southern bluefin tuna tracks in the eastern Great Australian Bight. The number of each fish indicates the start of its track. Symbols along tracks represent hourly positions (open symbol=day, solid symbol=night).

on the second day could not chum fish to the surface; the fishermen had also observed many tuna at the surface the previous day.

Tuna 4 was released near Ward Island on 30 January at 16:40 h and was tracked for 48 hours. This fish remained within the general area of release until tracking was terminated (Figs. 1 and 2B). Vertical behavior is shown in Figure 4B. The fish was associated with surface schools until night on the first day. It was also associated with large numbers of tuna (observed on the echosounder) throughout the night. The surface activity of tuna schools was low throughout the next day. Tuna were observed on the echosounder at the same depth as the tracked tuna throughout the day and next night, but not in the same numbers as the day before.

Tuna 5 was released on 13 March 1993 at 11:50 h at Rocky Island (Fig. 1). It was tracked for about 4 hours before it was lost. At 1500 h the tracked fish, together with other tuna, followed a pole-and-line vessel that was chumming at the time and that had crossed our path. The fish was temporarily lost but was relocated an hour later, again following the chum line of the pole-and-line vessel.

Tuna 6 was released at Rocky Island on 14 March 1993 at 07:35 h and subsequently tracked for 26 h (Figs. 1 and 2C). At 08:15 h the tracked tuna was observed following the chum line of the pole-and-line vessel (Fig. 5B). It was associated with other tuna at or near the surface until about 11:00 h. At 12:00 h the fish moved rapidly offshore at about 2.5 m/s and was tracked to the shelf. On reaching the shelf break, it remained within a region of warmer

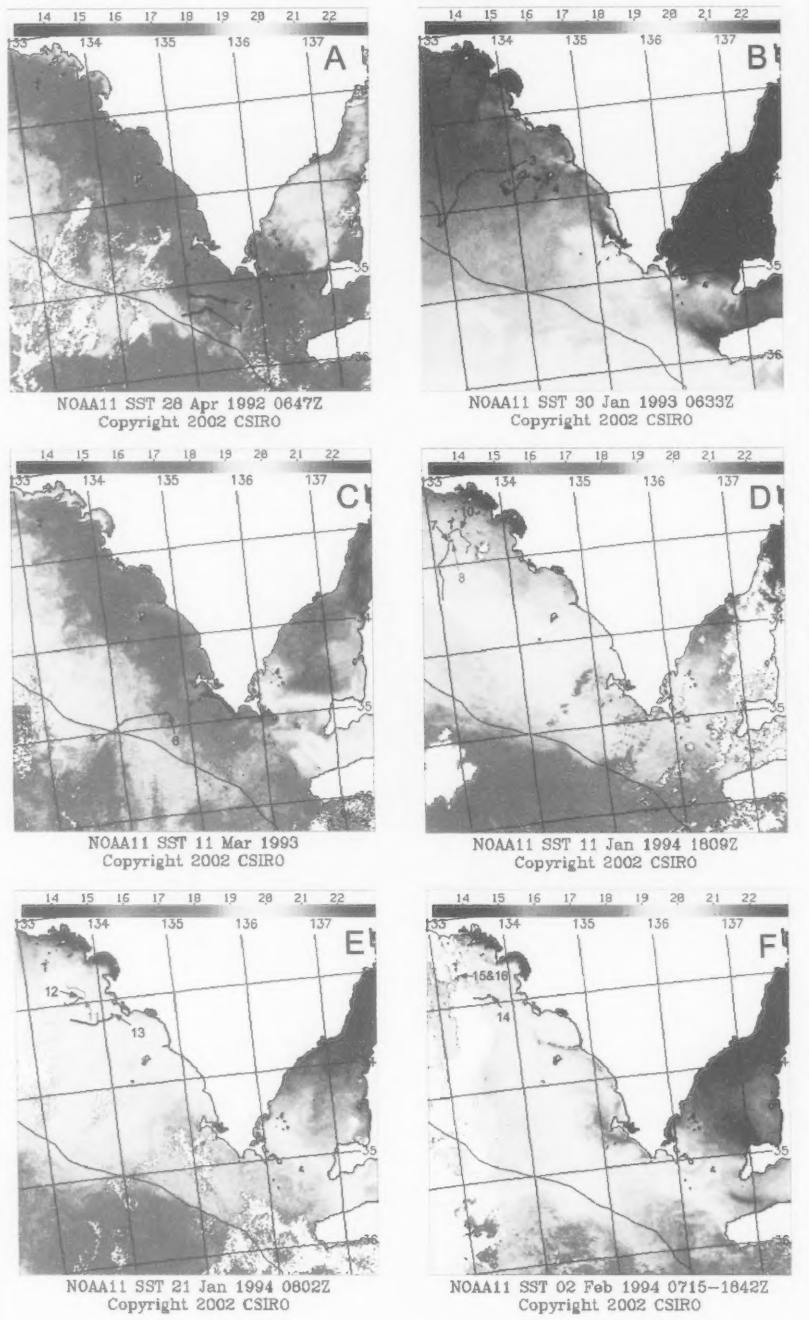

Figure 2

NOAA11 satellite sea-surface-temperature images of the study area during the periods of tracking with southern bluefin tuna tracks overlaid. (**A**) Tracks 1 and 2 on 29–30 April 1992. (**B**) Tracks 3 and 4 on 27–31 January 1993. (**C**) Track 6 on 14–15 March 1993. (**D**) Tracks 7, 8, and 10 on 10–16 January 1994. (**E**) Tracks 11–13 on 17–19 January 1994. (**F**) Tracks 14–16 on 31 January–2 February 1994.

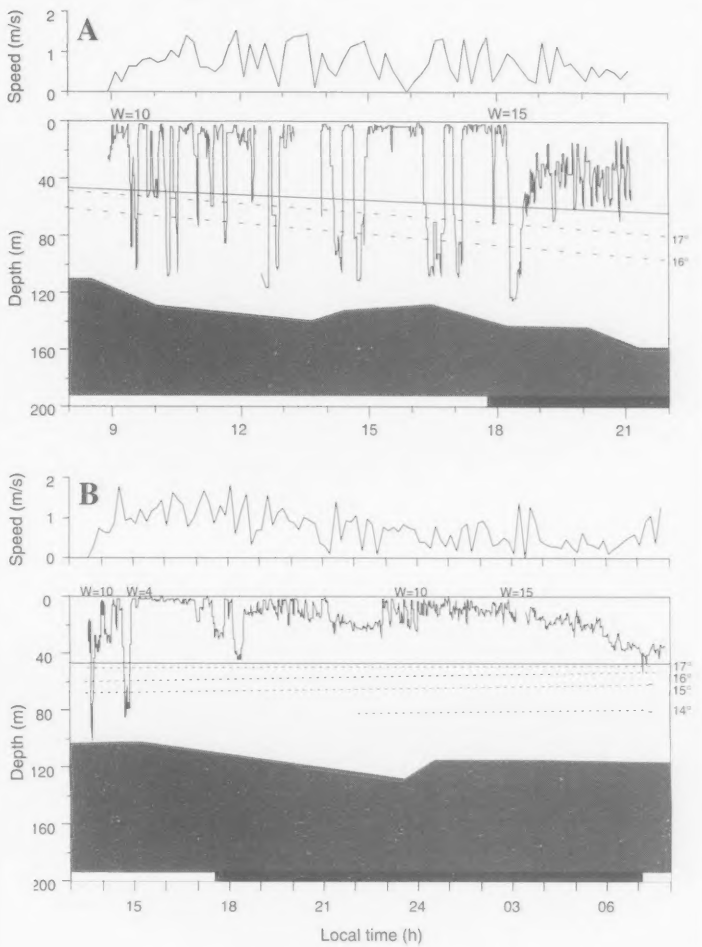

Figure 3

(**A**) Track of southern bluefin tuna 1 on 29 April 1992. (**B**) Track of southern bluefin tuna 2 on 30 April 1992. Speed over the ground (upper graph) and depth of the tuna (lower graph) are plotted against time. The sea bottom is indicated by shading, the solid line represents the bottom of the mixed layer and the dotted lines represent isotherms (°C). The black bar represents nighttime, the unshaded bar, daytime and W = wind speed in km/h.

surface water in association with a large subsurface school of tuna (Fig. 2C). While traveling to the shelf break, it remained near the bottom or just below the mixed layer. A deep sounding was made just after sunset and another just before dawn, the last reaching 180 m.

Tuna 7 was released at The Lumps 7 km south of Cannan Reef at 09:16 h on 10 January 1994 (Figs. 1 and 2D). This was the smallest fish tracked in this study. Unlike the others, it was caught on a trolled lure and landed after about a 5-minute struggle. Tracking was discontinued after 30 h due to bad weather. This fish was associated with large schools for the first five hours of tracking and again for three hours at first light the next day. It made postdusk and predawn dives (Fig. 6A).

Tuna 8 was released at The Lumps 7 km south of Cannan Reef at 10:58 h on 12 January 1994 (Figs. 1 and 2D). The fish was followed for 10 h until tracking was halted shortly after sunset. It remained in the upper 20 m for most of the track (Fig. 6B). At 12:50 h it followed the chum line of a pole-and-line vessel. From 14:00 to 16:00 h, it remained at the surface with a large school of tuna before slowing and sounding at a reef.

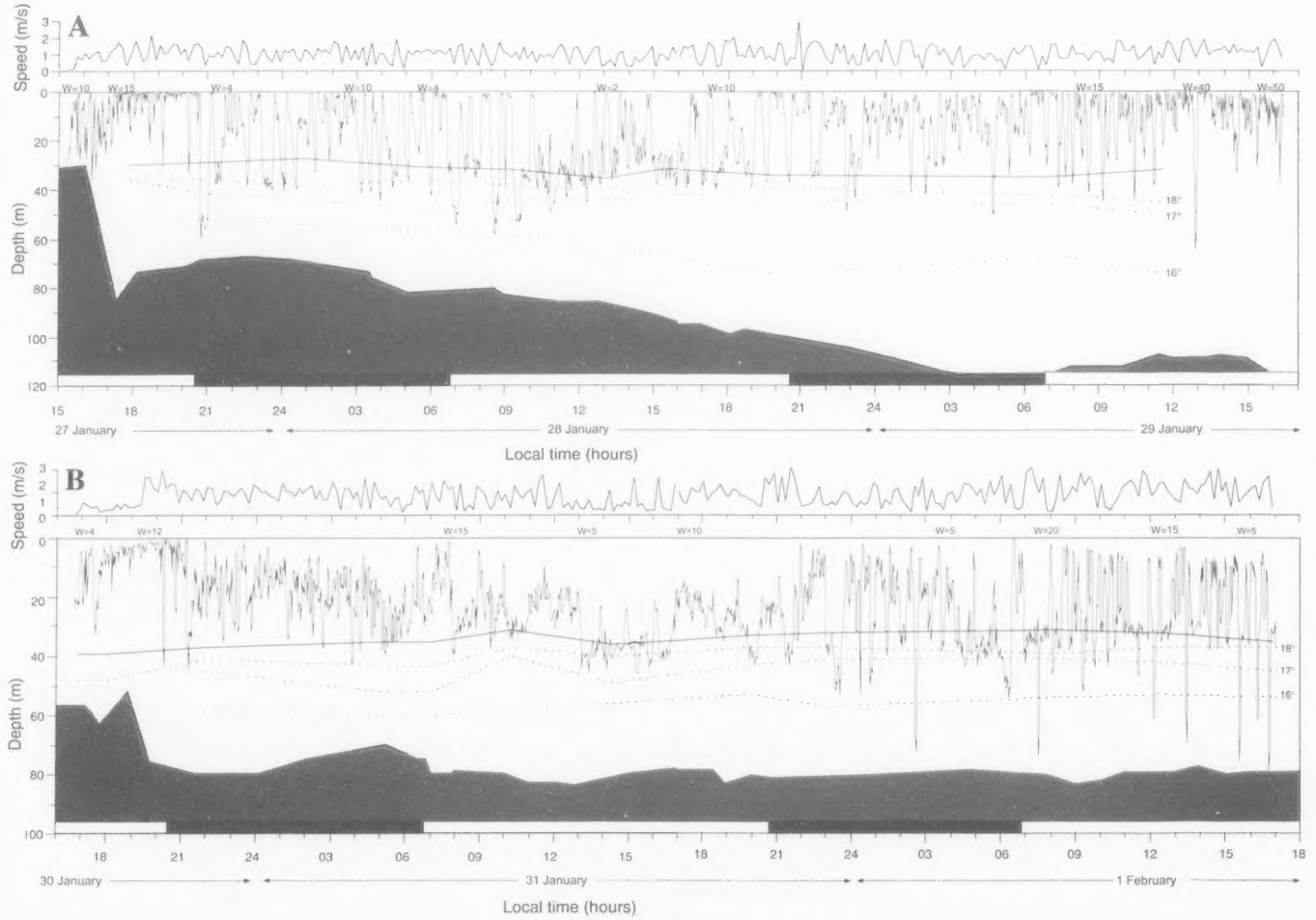

Figure 4

(**A**) Track of southern bluefin tuna 3 on 27–29 January 1993. (**B**) Track of southern bluefin tuna 4 on 30 January–February 1993. See Figure 3 for legend details.

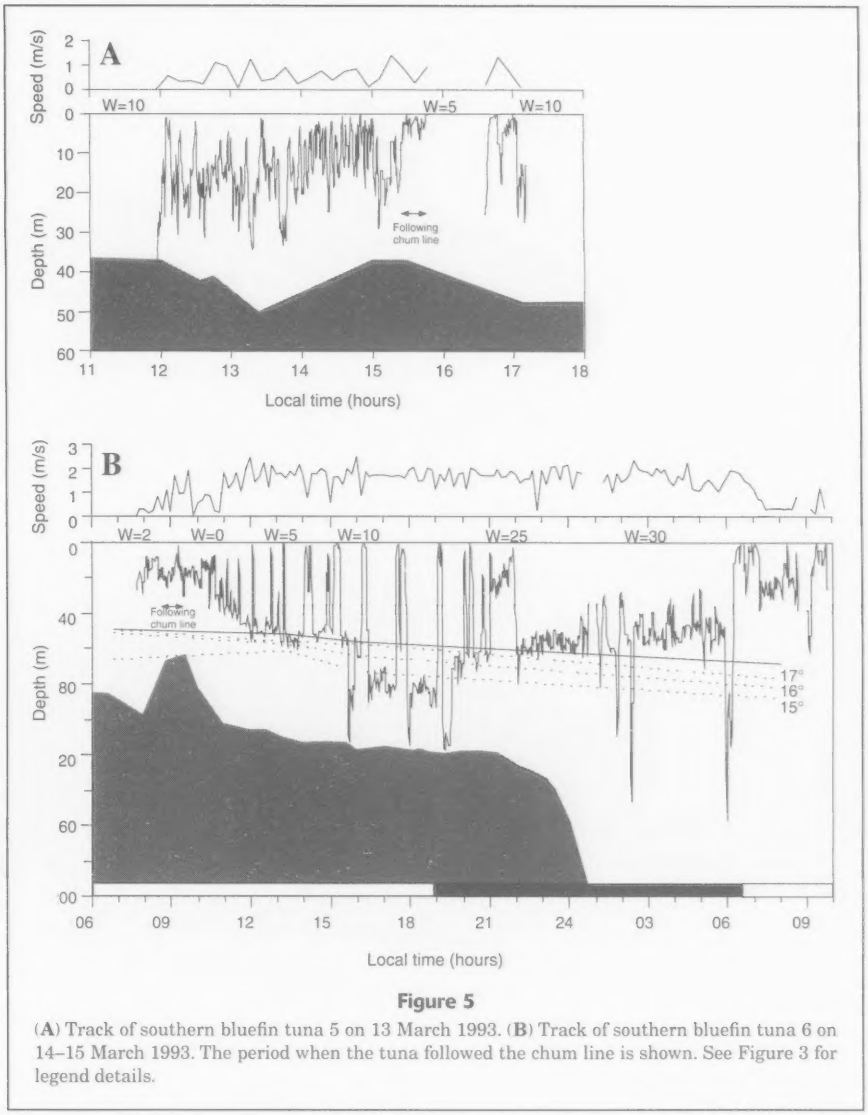

Figure 5

(**A**) Track of southern bluefin tuna 5 on 13 March 1993. (**B**) Track of southern bluefin tuna 6 on 14–15 March 1993. The period when the tuna followed the chum line is shown. See Figure 3 for legend details.

Tuna 9 struck at a tag during calibration experiments near Nuyts Reef at 09:05 on 15 January 1994 (Fig. 1). Consequently, it was tagged without leaving the water. The tag was either in the mouth or in the stomach. The tuna remained with tuna schools in the vicinity of tagging until 09:50 h and then moved away at considerable speed (2 m/s) for over an hour before sounding and slowing (Fig. 6C). It returned to the surface and remained there in association with a large surface school. The tag detached from the tuna at 1410 h.

Tuna 10 was released 11 km southeast of St Francis Island at 11:40 h on 16 January 1994. It was tracked for 13 h before it regurgitated the tag (Figs. 1 and 2D). The vertical movements of this fish differed from other tracks in that they were of relatively high amplitude (30+ m), traversed the water column, and were of moderate frequency (Fig. 7A). It spent little time at a particular depth, except for a short period at the bottom at the start of the track and again around 21:00 h. The fish was associated with tuna schools for most of the track. It made an extended dive just after sunset.

This was the first SBT to provide stomach-temperature data. The stomach temperature dropped rapidly initially, then increased to 25.4°C, which was about 6°C above water temperature. Temperature then decreased gradually for the rest of the track, but remained at least 4°C above ambient temperature.

Tuna 11 was released at The Lumps 41 km west of Sceale Bay at 13:57 h on 17 January 1994 with a temperature-pres-

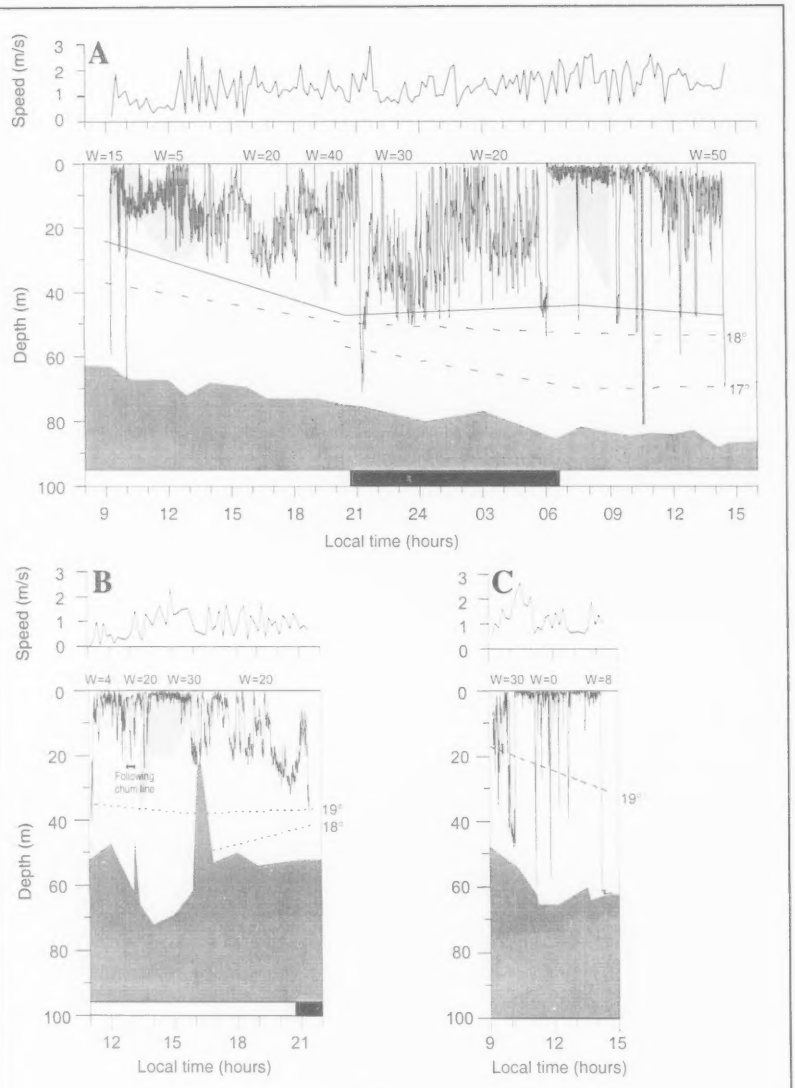

Figure 6

(**A**) Track of southern bluefin tuna 7 on 10–11 January 1994. (**B**) Track of southern bluefin tuna 8 on 12 January 1994. (**C**) Track of southern bluefin tuna 9 on 15 January 1994. Shading in the water column represents depth range of tuna schools detected by echosounder. See Figure 3 for other legend details.

sure tag in the stomach (Figs. 1 and 2E). This fish was associated with tuna schools for most of the track (Fig. 7B). Most vertical activity was oriented towards the surface, but periodic dives were made to or through the thermocline. At night the fish moved slightly deeper but continued to dive at regular intervals. It made an extended dive just after sunset.

The stomach temperature gradually increased through the night and by 01:00 h was at 28°C, which was 9°C above ambient temperature. At about 01:30 h there was a sudden drop in stomach temperature towards ambient temperature and then a gradual recovery that was most likely caused by the swallowing of prey or water (or both). The tag was regurgitated two hours later.

Tuna 12 was released at The Lumps 41 km west of Sceale Bay at 09:16 h on 18 January (Figs. 1 and 2E). It showed considerable vertical activity similar to tuna 10 and was associated with tuna schools throughout the track (Fig. 8A). It made an extended dive just after dusk.

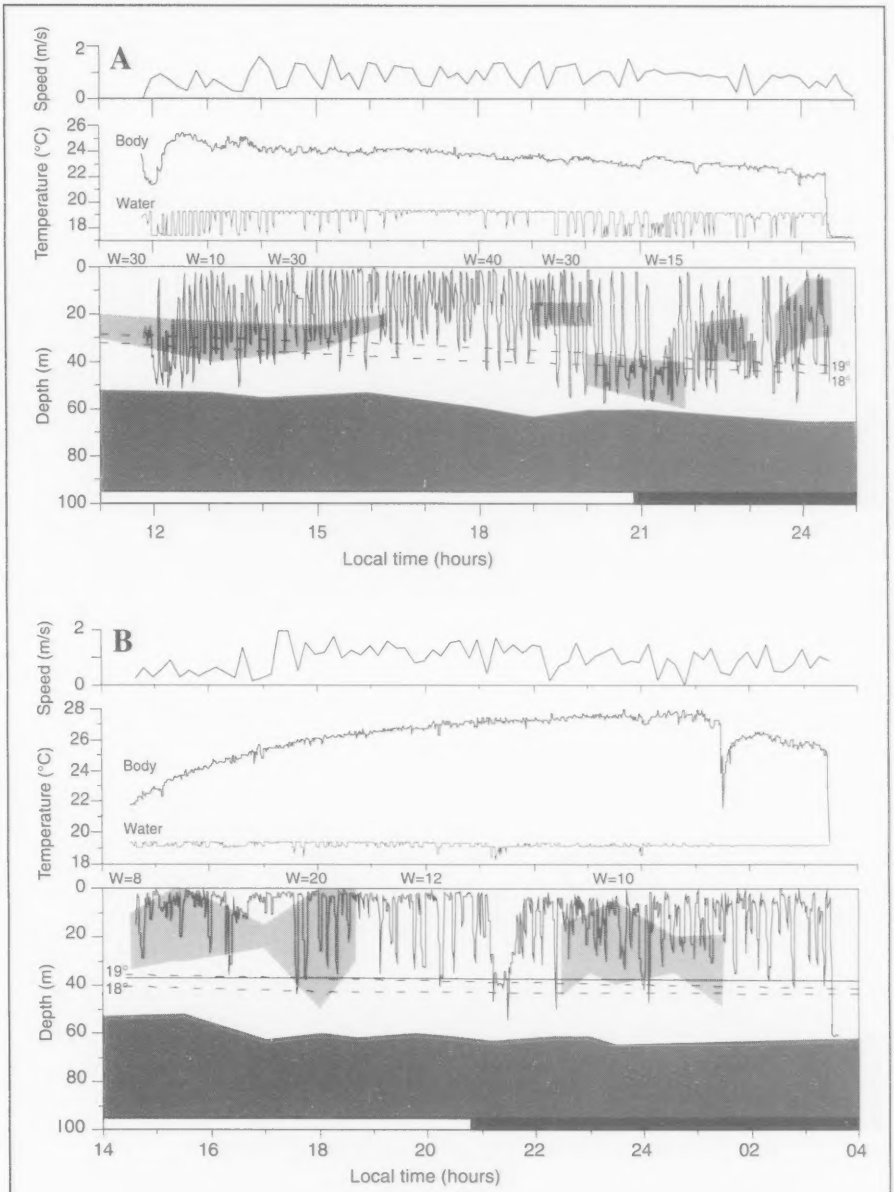

Figure 7

(**A**) Track southern bluefin tuna 10 on 16 January 1994. (**B**) Track of southern bluefin tuna 11 on 17–18 January 1994. See Figure 6 for legend details of upper and lower graphs. In the middle graph, stomach temperature and water temperature (interpolated from the depth of the fish and data logger temperature profiles) are plotted against time.

Tuna 13 was released 15 km west of Labatt Point at 1226 h on 19 January with a temperature-pressure tag in the stomach (Figs. 1 and 2E). This fish remained close to the surface during the day and deeper at the night, frequently staying just above the thermocline and sometimes diving through it. It made an extended dive after dusk and another just before dawn (Fig. 8B). It was associated with schools of tuna throughout the track. Although tuna schools did not appear on the echosounder during the afternoon, extensive bird activity and surface schools

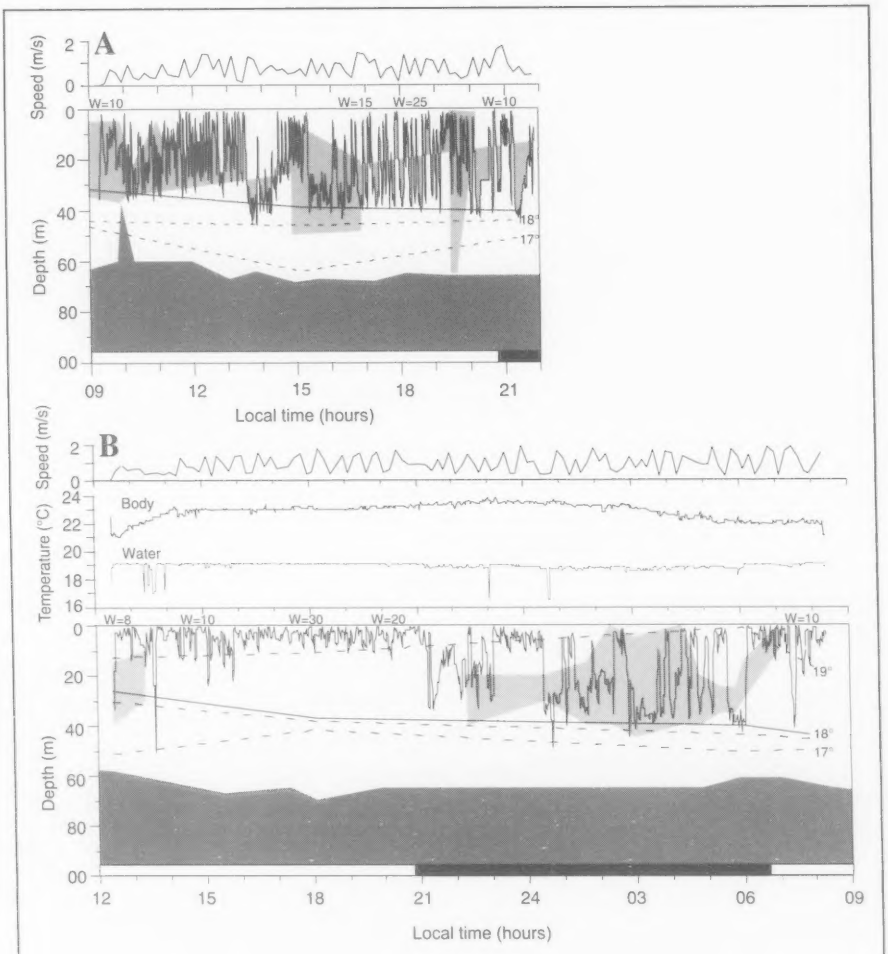

Figure 8

(**A**) Track of southern bluefin tuna 12 on 18 January 1994. (**B**) Track of southern bluefin tuna 13 on 19 January 1994. See Figure 7 for legend details.

of tuna were observed during the whole period that the tracked tuna was near the surface.

Stomach temperature showed a marked drop initially (presumably it swallowed water on its release) and then a gradual recovery. Temperature reached a peak of 23.8°C, about 4.5°C above ambient temperature, near midnight and then slowly declined throughout the remainder of the night.

Tuna 14 was released 41 km west of Sceale Bay at 12:26 h on 31 January 1994 (Figs. 1 and 2F). The tuna was lost for about 20 minutes early in the track (Fig. 9A). It had moved south before doubling back and returning to the reef where it had been tagged. At 16:40 h it then swam away with a school of tuna, remaining just above the thermocline and occasionally making excursions to the surface. It made an extended dive after dusk.

Tuna 15 was released at The Lumps 7 km south of Cannan Reef at 13:26 h on 1 February 1994 (Fig. 1). It joined a large school of tuna following the chum line of a pole-and-line vessel, but was lost one hour later.

Tuna 16 was released at The Lumps 7 km south of Cannan Reef at 09:30 h on 2 February 1994 (Figs. 1 and 2F). It was associated with schools initially, but they dispersed at about 1400 h (Fig. 9B). The tag was regurgitated at 15:20 h.

Time at depth

The proportion of time spent by tuna in 5-m interval depth strata was plotted by day and night for all tracks combined (Fig. 10). These data indicated that SBT are surface-oriented by day in the Great Australian Bight, spending a significant

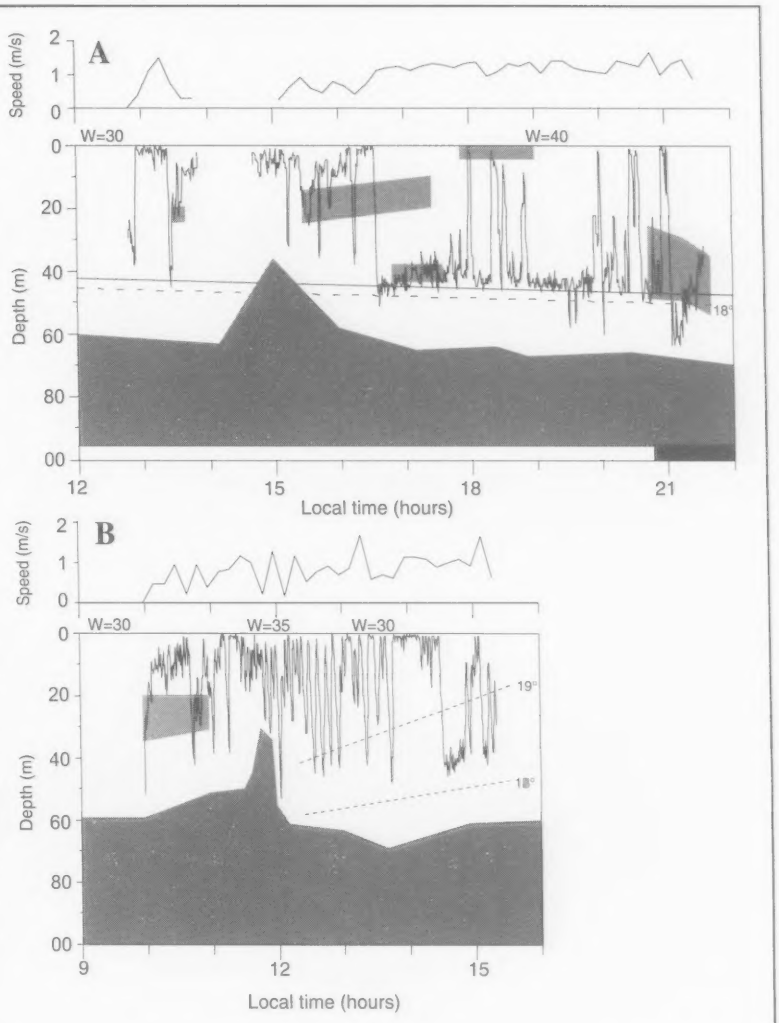

Figure 9

(**A**) Track of southern bluefin tuna 14 on 31 January 1994. (**B**) Track of southern bluefin tuna 16 on 1 February 1994. See Figure 6 for legend details.

proportion of their time (nearly 30%) in the upper 5 m. At night they tend to remain somewhat deeper, although they are present at the surface for part of the night. Tunas 4 and 12 were not surface-oriented during the day, but ranged evenly within the mixed layer. Both these fish were associated with large schools throughout the track and they exhibited rapid vertical oscillations, which we assumed spanned the vertical boundaries of the school. Tuna 6 also spent little time at the surface. It was associated with a small school of tuna and spent most of its time at or below the thermocline while travelling at 2.5 m/s towards the shelf edge. Tuna 14 also spent much of its time at the thermocline boundary while traveling during the day.

Swimming speed

The average swimming speeds of SBT over the entire tracks were in the range of 0.5–1.4 m/s or 0.5–1.4 body lengths/s. These speeds are based on the movements of the tracking vessel and therefore are considered conservative because they do not incorporate the horizontal or vertical meandering of the tracked fish or water currents. There were small differences in the mean speeds between day (0.90 m/s) and night (0.94 m/s) for all fish combined. The frequency distribution of these speeds differed markedly between day and night (Fig. 11). However, the number of observations during the day (n=1119) far exceeded those

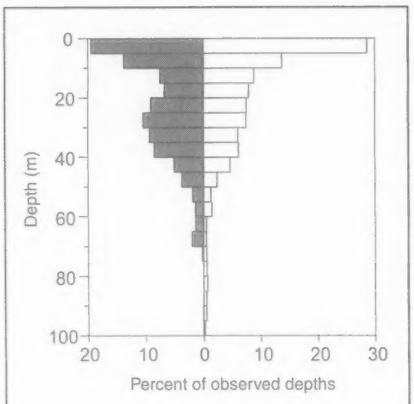

Figure 10

Distribution of observed depths (5-m intervals) by day (open bars) and night (shaded bars) for all tracked southern bluefin tuna.

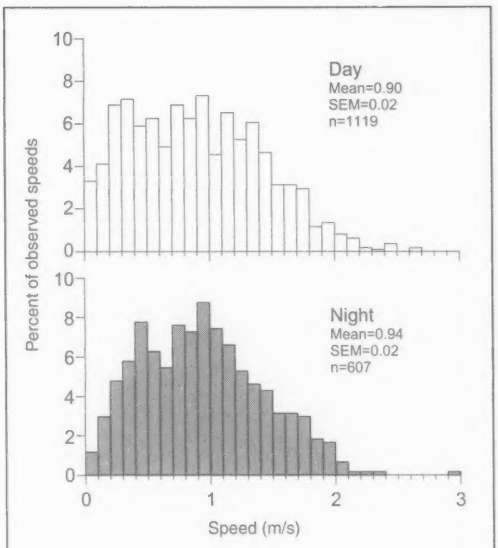

Figure 11

Distribution of observed speeds over the ground (0.1 m/s intervals) by day and night for all tracked southern bluefin tuna.

at night (n=607) and probably accounts for much of the difference in distributions.

Discussion

Horizontal movements

The average swimming speeds of SBT over entire tracks of 0.5–1.4 body lengths/s were similar to the range of mean speeds (0.6–1.0 body lengths/s) for Atlantic bluefin tuna (Lutcavage et al., 2000) and 1.02–1.34 body lengths/s for Pacific bluefin tuna (Marcinek et al., 2001). This is within the range of minimum speeds (0.5–2.0 body lengths/s) required to maintain hydrostatic equilibrium in scombrids (Magnuson and Weininger, 1978). A much higher sustained swimming speed of 2.5 m/s was recorded for tuna 6, which traveled at this speed for 18 hours, virtually in a straight line, from Rocky Island to the shelf break. The vertical movements of this fish were minimized by it orienting itself with the thermocline interface or the surface. And horizontal movements were not apparent. A speed of 2.5 m/s or 2.6 body lengths/s is probably a realistic sustained swimming speed for SBT. Although tunas are obviously capable of high bursts of speed, sustained swimming speeds seem to be very much lower. Yellowfin tuna have been tracked at speeds of 1.2–3.5 body lengths/s, and bigeye tuna at 1.4 body lengths/s (Holland et al., 1990a, Block et al., 1997). The sustained swimming speeds of Atlantic bluefin tuna, determined from sequential aerial photographs, were 0.8–1.6 body lengths/s (NOAA[6]). Brill (1996) considered that the specialized anatomy, physiology, and biochemistry of tuna evolved, not for high burst and sustained swimming speeds as proposed by Dickson (1995), but for rapid growth, digestion, and recovery from exhausting activity.

The horizontal movements and distribution of SBT suggest strong associations with regions of topographical variation or higher temperatures (or both). The SBT were in the warmer waters of the NW region of the study area in 1994, and the tracked fish also remained within areas of warmer water. In 1992 and 1993, all the tuna that traveled some distance swam to waters of similar or higher temperatures. Lutcavage et al. (2000) found that tracked North Atlantic bluefin tuna also traveled on the warm side of surface fronts and that offshore movements were generally associated with offshore warming of deep basins.

The temperatures measured during tracking sometimes did not match up with satellite sea-surface temperatures, owing to the inability of sea surface temperature (SST) algorithms to correct for the variability in atmospheric water vapour, cloud, and aerosols, etc. However, the relative temperature differences considered here appear to be robust. Within these temperature limitations, the tuna were initially located on lumps or near islands. Migration to new areas was often interrupted by brief stays at lumps on the way. The shelf break was clearly the destination of tuna 6. It was tracked near Rocky Island for three hours, before it left abruptly and moved in a straight line to

[6] NOAA (National Oceanic and Atmospheric Administration). 1975. A study of the applications of remote sensing techniques for detection and enumeration of giant bluefin tuna. Southeast Fish. Cent. contrib. no. 437 (MARMAP no. 108), 48 p. National Space Technology Laboratories, Bay Saint Louis, Mississippi 39520.

the shelf break, which it reached some 18 hours later. It remained in that area until tracking ended. These lump, reef, island and shelf-break associations matched the distribution of sightings by aerial survey (Cowling et al.[7]).

Surfacing behavior

Most SBT spend a large part of the day in the upper 10 m (Fig. 10) in the Bight in summer unless they travel to other areas. At night, they tend to move to deeper water, but some tracked tuna remained in the upper 10 m throughout most of the night. The relatively long time spent at the surface during the day in the Bight (nearly 30%) would facilitate sightings by aerial survey, and surfacing behavior would significantly influence aerial detection.

The surface behavior of southern bluefin tuna in the Bight contrasts with that of most other tunas studied. Yellowfin tuna near Hawaii have an average daytime depth of 71 m during tracks offshore and away from fish aggregating devices (FADs), with modes at 0–10 m and 50–60 m. When near FADs, they have an average daytime depth of 59 m. At night, yellowfin have modes at 0–10, 30–40, and 180–190 m (Holland et al., 1990a). Similar depth distributions for yellowfin tuna were observed in the western Pacific (Yonemori, 1982). In the eastern Pacific Ocean, at the northern extent of their range, yellowfin tuna remained at somewhat shallower depths during the day than in previous studies (Block et al., 1997), presumably because of the shallowness of the mixed layer which limited their depth distribution. In the western Indian Ocean, yellowfin tuna tracked both on and off FADs spent most of the day between 60 and 110 m (Cayré and Chabanne, 1986; Cayré, 1991; Marsac et al.[3]).

Tracked skipjack tuna spent little time at the surface during the day in waters off Hawaii (Yuen, 1970; Dizon et al., 1978), and Tahiti (Cayré and Chabanne, 1986), although they were surface oriented at night. In the western Indian Ocean, two skipjack tuna tracks were found at somewhat shallower depths but the modal depths were still between 10 and 20 meters (Cayré, 1991). Bigeye tuna tracked off Hawaii had a modal depth of 220 m during the day and 80 m at night (Holland et al., 1990a). Atlantic bluefin tuna appear to spend some time near the surface in inshore waters off the New England area (Carey and Lawson, 1973), although the modal depth of 0–15 m during the day (Lutcavage et al., 2000) is somewhat deeper than that for SBT in the Great Australian Bight. This nearsurface orientation of Atlantic bluefin tuna has prompted development of aerial surveys to assess the abundance and distribution of these tuna in these waters (Lutcavage and Kraus, 1997). The extensive surfacing behavior of SBT in the Bight does not appear to occur in the shelf waters of the Indian Ocean off Western Australia. Of the six SBT tracked in the west, only one spent significant time at the surface during the day (Fishery Agency of Japan[4,5]). However, this fish oscillated rapidly between 0 and 40 m rather than remaining near the surface. The different surfacing behavior of these SBT in the west may have been due to their much smaller size (35–48 cm compared to 67–114 cm), and that they were in a migratory mode moving southwards, assisted by the Leeuwin Current (Shingu, 1967; Maxwell and Cresswell, 1981), rather than in summer residency.

The conditions in which SBT come to the surface in the Great Australian Bight are quite varied. These tuna remain within the surface 5 m for extended periods during the day under a range of weather and sea conditions, although surfacing is more pronounced on warm days with little wind. A clear example of this type of movement was evident with tuna 9, which remained below the surface in a school of tuna for the first hour of the track, during which winds were documented at over 35 km/h. After the winds dropped, the tracked tuna surfaced and remained there, apart from occasional dives, for the rest of the track. Surface schools of tuna were observed as far as the eye could see during these calm conditions. In contrast, extensive surfacing can occur in adverse weather, as observed in fish 7 between 07:00 and 09:00 h during rough seas and winds >35 km/h. However, in these conditions, no surface fish could be seen from the vessel. Protocols for aerial surveys of SBT in the Bight restrict surveys to wind speeds of <18 km/h because of a marked decrease in school sightings at higher wind speeds (Cowling et al.[7]). The highest number of sightings per unit of effort occurred when aerial surveys were flown in conditions of low wind speeds and little cloud cover. The ultrasonic telemetry suggests that wind affects detection of schools from the air rather than their surfacing behavior.

One of the objectives of the aerial survey was to reduce uncertainty in aerial survey estimates of surface abundance by incorporating environmental and behavioral data into the aerial survey analyses. Although the results from ultrasonic tracking provided preliminary information on vertical distribution that might affect sighting by aerial survey, the intent of our study was to use the more extensive data that would be obtained from archival tags to model responses in surfacing behavior to environmental conditions through space and time. Aerial survey estimates of abundance could then be adjusted by incorporating the proportion of time that SBT would be visible during aerial surveys based on the environmental conditions that occurred at the time of survey flights.

A distinct surfacing behavior regarded as a characteristic of SBT in the Bight during summer is called "rippling" (Hynd and Robins, 1967). This behavior occurs under very calm, sunny conditions. Tuna laze at the surface for extended periods, often breaking this inactive phase by rolling from side to side. Unfortunately we did not have suitable weather conditions to observe this behavior. However, data from archival tags suggest that these fish derive significant heating benefits through both insolation and the transfer of heat from the warm surface waters (Gunn et al.[2]).

[7] Cowling, A., T. Polacheck, and C. Millar. 1996. Data analysis of the aerial surveys (1991–1996) for juvenile southern bluefin tuna in the Great Australian Bight. 1996 Southern bluefin tuna recruitment monitoring workshop report. Rep. RMWS/96/4, 87 p. CSIRO Marine Laboratories, Castray Esplanade, Hobart, Tasmania, Australia 7000.

Reference depths

Reference depths—the depths to which tuna return after regular excursions above or below them—are not well defined in SBT in the Bight. Bounce dives from the surface occur in tracks 1, 3, and 11, and brief excursions above and below the bottom of the mixed layer could be seen in parts of tracks 4, 6, and 14. None of these showed the movements characteristic of bigeye tuna, which use the 15–16° isotherm as a reference point and make regular excursions to the surface (Holland et al., 1990a). These excursions are thought to be a way of regaining optimum body temperature after foraging in cooler deep water (Holland et al., 1990a; Holland et al., 1992). Bluefin tuna have a more advanced vascular anatomy for physiological thermoregulation than bigeye tuna (Holland et al., 1992); therefore one would expect SBT to display less pronounced behavioral thermoregulation than bigeye tuna under the same thermal regime. Unfortunately, the temperature range of the shallow waters of the Bight was also not large enough to induce such a response.

The interface of the surface mixed layer and the thermocline is a reference point used by many tuna species. Yellowfin tuna often remain within this narrow depth band, especially when travelling in a straight line (Carey and Olsen, 1982; Holland et al., 1990a). Traveling fish have been observed to alternate abruptly between the thermocline interface and the surface, which might assist in straight-line orientation (Holland et al., 1990a). Tracks 6 and 14 provide the clearest examples of use of the thermocline interface during sustained straight-line migration. Tuna 6 remained at a depth of about 20 m while staying in the area. However, once it started swimming toward the shelf break, it maintained a relatively constant depth within or just above the thermocline. While this behavior is apparently a characteristic of yellowfin tuna travelling alone (Carey and Olsen, 1982), our tracks were for SBT travelling in schools. Tunas 7 and 8 remained at the surface during fastest straight-line swimming, suggesting that both depth zones might be used during straight-line swimming. Although it appears that the thermocline interface provides some advantage to sustained straight-line movement, it is not clear whether the advantage is in orientation: possibly this temperature range balances heat build-up from sustained swimming.

In contrast to returning to a reference depth, some tracked fish oscillated rapidly within a depth band. This behavior was observed in parts of tracks 4, 7, 10, and 12. This "frenzied" activity might be ascribed to disturbed behavior caused by the tagging or tracking (or both). However, this behavior might reflect individuals traversing the vertical boundaries of the school (Carey and Olsen, 1982). When this behavior was observed in our study, the tracked fish appeared to be part of a school. However, there were many times when the fish was in a school but rapid vertical oscillations were not apparent. Possibly the schools did not extend over sufficient depth range to make this behavior obvious.

Predawn and postdusk dives

A feature of many of the tracks of SBT was the deep dive made just before dawn as the sky began to lighten, and just after sunset before all light was gone. In these dives, the tuna descended rapidly, stayed a short time at the bottom of the dive, and then usually rose gradually to its original depth. These signature dives were observed in tracks 1, 3, 4, 6, 7, 11, 12, 13, and 14 and possibly occurred in other cases obscured by repeated dives over the twilight period. Archival tag data showed clear signature dives in the Bight and more varied behavior off the shelf (Gunn et al.[2]). They also showed that in the central Indian Ocean, SBT dive at dawn, remain at great depth throughout the day feeding on squid, and return to the surface at night. The dawn dives we tracked might correspond to the first part of this movement, but the shelf waters of the Bight are too shallow to have a significant scattering layer, and therefore usually do not allow for the detection of prey. Perhaps this dive at dawn is a fixed behavior that has evolved to locate the scattering layer when SBT are in waters of sufficient depth.

If tuna rely largely on sight to locate prey, twilight would be the first opportunity (dawn), and last opportunity (dusk), in which to find the scattering layer as it rises during the night and descends during the day. Dawn and dusk dives have been observed in eastern spotted dolphin in the eastern tropical Pacific Ocean (Holland[8]). During the day, these dolphin remained in the shallow mixed layer (10–15 m). However, at late dusk they dived to depths of about 65 m. These were followed by further dives, each one a little shallower than the last, until diving was again largely confined to the mixed layer. Just before dawn the pattern was reversed. A line drawn along the bottom of the dives from dusk to dawn would describe a bell shape. The dolphins' behavior was thought to be in response to the vertical movement of the scattering layer. Dawn and dusk dives have since been noted in Atlantic bluefin tuna tracked in shelf waters off New England (Lutcavage et al., 2000) and are apparent in tracks of Pacific bluefin tuna in the eastern Pacific (Marcinek et al., 2001). Block et al. (1997) reported predawn dives in yellowfin tuna tracked in the California Bight. Their vertical track plots suggested that postdusk dives may also occur. Similar vertical behavior has been apparent in the track of one skipjack (Cayré and Chabanne, 1986) and one yellowfin tuna (Carey and Olsen, 1982). However, the absence of similar dives in other studies suggests that the timing of the dives was coincidental.

Stomach temperature

Muscle and stomach temperatures of Atlantic bluefin tuna were monitored in several tracking experiments (Carey and Lawson, 1973; Carey et al., 1984). Both were shown

[8] Holland, K. N. 1996. Personal commun. University of Hawaii, PO Box 1346, Coconut Island, Kaneohe, Hawaii 96744.

to be well above ambient water temperature. Stomach temperature increased after feeding, which was attributed to the hydrolytic processes of digestion and an increase in metabolic rate. Possibly raised stomach temperature speeds digestion and enables a higher feeding frequency when food is abundant. The capacity to maintain higher stomach temperature is enhanced by thermal isolation through heat exchangers, the gas bladder, and the fatty body wall (Carey et al., 1984). Therefore, stomach temperature would reflect activities associated with feeding and digestion, rather than temperature changes occurring in the body. SBT, while very much smaller than the giant bluefin tuna tracked by Carey, also showed a marked differential between stomach and ambient temperatures. The largest differential of 9°C (track 11) was found in the largest SBT tracked, which may be relevant. Because temperature increased steadily during the track, it was probably due to digestion of a meal. All pole-and-line–caught SBT tracked during these experiments were initially chummed with pilchards and could have eaten pilchards just before tracking. In some instances, tunas regurgitated pilchards while the tag was placed in their stomachs. A caecal temperature differential reaching 10°C has also been observed in a 103-cm SBT after being fed in cage experiments (Gunn et al.[9]). The smaller temperature differential observed in the other two tracked tuna (tuna 10 and 13) may have been a consequence of their having less food in their stomach to digest, or their smaller size.

Tuna 11 showed the characteristic changes in stomach temperature associated with the swallowing of prey or water or both. Two swallowing events occurred, a minute apart, resulting in a drop in stomach temperature to ambient temperature. Stomach temperature recovered rapidly, but not quite to the level before swallowing. Carey et al. (1984) managed to have Atlantic bluefin tuna retain tags in their stomachs for up to 13 days by feeding them to ensure that their stomachs never remained empty. Several hours before regurgitation of the tag, a series of cold pulses were observed in stomach temperature, presumably from swallowing water which lowered the stomach temperature briefly. If these cold pulses persisted, the tag would be spat out a few hours later. If the tuna was fed, the tag was usually retained. If regurgitation to purge indigestible items from the stomach normally occurs after digestion is complete and the stomach is relatively empty, as suggested by Carey et al. (1984), then it is likely that the swallowing events observed in tuna 11 involved little or no food. Because a very marked drop in stomach temperature was observed in tuna 11, a large amount of water must have been swallowed.

[9] Gunn, J., T. Polacheck, T. Davis, M. Sherlock, and A. Betlehem. 1994. The development and use of archival tags for studying the migration, behaviour and physiology of southern bluefin tuna, with an assessment of the potential for transfer of the technology to groundfish research. Proc. ICES mini-symposium on migration, St. Johns, Newfoundland. ICES C.M. Mini:2.1, 23 p. International Council for the Exploration of the Sea, Palægade 2-4, DK-1261 Copenhagen K, Denmark.

The effects of chumming on tuna behavior

Observations on tracked tuna being caught up in chumming by commercial pole-and-line fishing have provided us with insights into these operations. Tunas 5, 6, 8, and 15 were associated with chum lines for part of their tracks. They all followed the chum line at a depth of about 20 m for 15–30 minutes, and some came to the surface for brief periods. The tuna schools extended to at least 200 m behind the vessel that was chumming. Pole-and-line operators usually steam forward at about 2 m/s, chumming with live and, sometimes, frozen pilchards. They progress from tuna school to tuna school hoping to combine schools. Most tuna appear to be below the surface and well behind the boat. Fish progress to the front of the school and come to the surface to take chum, replacing tuna that were there before them. Based on our tracking, it appears that tuna after spending a short time at the surface, break away from the chum line in groups or in schools.

Effects of tagging and tracking on tuna behavior

There is a concern that capture, tagging, and tracking procedures change the behavior of the fish being observed. A number of criteria are used to support the view that the fish behave normally: they remain within a school (Yuen, 1970; Cayré, 1991; Cayré and Marsac, 1993); show similarity in vertical and horizontal movements across tracks (Holland et al., 1990a; Cayré, 1991) or through experimental procedures such as evaluating swimming performance when tags are attached externally (Arnold and Holford, 1979; Blaylock, 1990) or observing food consumption when tags are placed in the stomach (Lucas and Johnstone, 1990).

There is however, evidence that SBT do react adversely to being tagged. Hampton (1986) found that lower than expected numbers of SBT tagged with dart tags were recaptured in the first 5 days after release. Also, recaptured fish were in significantly poorer condition than untagged fish—the effect being greatest in those at liberty for 5–20 days (Hampton, 1986) and 13–24 days (Hearn, 1986). Presumably, the adverse effects were related to reduced feeding.

Fish generally undergo a phase of recovery from the trauma of capture and tagging. The resumption of "typical" behavior is often taken as a sign that the fish is behaving normally (Holts and Bedford, 1990). In our study, five tuna initially dived to the bottom, five dived below the depth distribution of the tuna school, and six returned immediately to the school. All returned to schools, which were usually near the surface, within 20 minutes. Most significantly, four tracked tuna actually joined the chum lines of commercial pole-and-line vessels shortly after tagging. However, it could not be determined whether these four tuna were feeding because they did not have temperature-pressure tags in their stomach.

Stress associated with capture and tagging is more obvious in larger fish: blue and striped marlin remain at depth for many hours before returning to normal depths

(Holland et al., 1990b; Holts and Bedford, 1990; Block et al., 1992a). Black marlin dive after release but usually return to normal depths soon after (Pepperell and Davis, 1999). High, sustained, swimming speeds for up to the first six hours of blue marlin tracks were attributed to increased ram ventilation to reduce anaerobic debt (Block et al., 1992b). Undoubtedly there is trauma associated with capture and tagging, but pole-and-line capture is fast, and SBT are not as tired as they would be if caught on a rod and line. In most of the SBT tracks, swimming speed was much slower in the half hour after release than for the remainder of the track. Possibly this slow swimming relates to a recovery phase. However, it more likely reflects the nature of pole-and-line fishing and the association of the chummed school with the boat. After catching and releasing the fish, chumming is stopped. However, the school usually remains with the boat for a short period. The strong schooling behavior of SBT appears to quickly override trauma-induced behavior, such as remaining at depth, that might keep tagged fish away from the school.

Association of the tracked fish with schools is probably the most encouraging sign to the field worker that the tuna is behaving normally, or at least that its movements are representative of the school as a whole. This association was marked in our study. However, on the occasions when the tracked fish appeared to be alone, it was not clear whether this isolation was due to the normal breakup and dispersal of the schools aggregated by the chumming operation or to the tagging and tracking procedure. We were concerned that "herding" (the vessel following the fish influencing the direction of its movements) over a period of time might separate a fish from its school. However, it is also not clear whether it is possible to detect if the tracked fish is solitary or with a school. Depending on the skill and knowledge of the observer, schools can usually be detected in good weather if there is surface or subsurface activity. At night or in rough seas, the usual way of detecting schools is by echo-sounder, but this works only if the school is under the tracking vessel. The school must therefore be large and extend well behind the tracked fish (which is nominally tracked at a distance of 400 m). Often "solitary" tracked tuna displayed the repeated and predictable behaviors seen in other SBT tracks and generally accepted as criteria of "normal" behavior, the most striking of which are the predawn and postdusk dives.

Three methods of tag attachment were used in our study—five tags were attached externally behind the second dorsal fin, ten were placed internally in the stomach, and one tag was accidentally struck by a free-swimming tuna and was attached by the force of the strike. The effects of attaching tags are not currently quantifiable because of the diversity of tuna behaviors. However, the tracks of SBT with stomach tags were more dynamic than the tracks of tuna with tags attached externally. Tunas with stomach tags seemed more responsive to their environment: their behavior included fast, sustained swimming, large translocations, and these tuna were frequently observed with other tuna attracted by chumming operations. Externally attached tags presumably created physical disturbances, such as drag, turbulence, and attachment wounds to which the tuna had to adjust. These are more likely to cause short-term disturbance in behavior than swallowed tags. However, stomach tags had unpredictable, and often short, retention times, which counteracted their advantages.

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Turtle excluder devices—Are the escape openings large enough?*

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Abstract—All five species of sea turtles in continental U.S. waters are protected under the Endangered Species Act of 1973 and the population sizes of all species remain well below historic levels. Shrimp trawling was determined to be the largest source of anthropogenic mortality of many of the species. As a mechanism to reduce the incidental catch of turtles in trawl nets, turtle excluder devices have been required intermittently in the shrimp fishery since 1987, and at all times since 1994. The expanded turtle excluder device (TED) regulations, implemented in 1994, were expected to reduce shrimp trawl capture of sea turtles by 97%. Recent evidence has indicated that the sizes of turtles stranding were not representative of the animals subjected to being captured by the shrimp trawlers. The purpose of our study was to compare the sizes of stranded sea turtles with the size of the TED openings. We compared the sizes of stranded loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and Kemp's ridley (*Lepidochelys kempii*) sea turtles, the three species most commonly found stranded, to the minimum widths and heights of TED openings. We found that annually a large proportion of stranded loggerhead turtles (33–47%) and a small proportion of stranded green turtles (1–7%) are too large to fit through the required minimum-size TED openings. The continued high mortality of sea turtles caused by bottom trawling is reason for concern, especially for the northern subpopulation of loggerhead turtles, which currently is not projected to achieve the federal recovery goal of reaching and maintaining prelisting levels of nesting.

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Fish. Bull. 100:466–474 (2002).

All five species of sea turtles in continental U.S. waters are protected under the Endangered Species Act of 1973 (ESA, PL93-205). Elasticity models of turtle populations have indicated that the life stages with the highest elasticity are juveniles (i.e. a reduction in mortality in these stages would result in the greatest annual population multiplication rate) (Crouse et al., 1987; Crowder et al., 1994; Heppell, 1998a, 1998b; Epperly et al., 2001; Heppell et al., in press). Size data indicate that the sea turtles most often found dead on ocean beaches are immature (Crouse et al., 1987; STSSN[1]) and shrimp trawling is thought to account for the majority of these deaths (Magnuson et al., 1990; Caillouet et al., 1991, 1996; Crowder et al., 1995). Strandings, however, likely represent only a small proportion of the animals that die offshore (TEWG, 1998).

Beginning in the fall of 1987, the National Marine Fisheries Service (NMFS) seasonally required turtle excluder devices (TEDs) in shrimp trawl nets on most vessels operating in ocean waters off the southeastern U.S. as a mechanism to reduce the incidental catch of turtles in general and the catch of the large immature turtles in particular (Federal Register, 1987); vessels operating off Cape Canaveral and off southwest Florida were required to use TEDs all year. Boats working in inshore waters were allowed to use tow time limits in lieu of TEDs. The difference between offshore and inshore regulations was due, in part, to the lack of information on the distribution and abundance of sea turtles in inshore waters and to the lack of documentation of incidental captures by shrimp trawlers working in these inshore waters (Federal Register 1992a). For the first few years implementation of the regulations was delayed by challenges in the courts and in Congress. The regulations were implemented fully in Spring 1990.

Evidence of the importance of inshore areas to sea turtles, along with evidence that shrimp trawlers catch sea turtles in inshore waters (Epperly et al., 1995; NMFS[2]) provided sufficient justification for NMFS to expand requirements for turtle excluder devices in the shrimp fishery to all areas at all times, including inshore waters; full implementation of these requirements was achieved by December 1994 (Federal Register, 1992a, 1992c). The expanded TED regulations were expected to reduce shrimp trawling capture of sea turtles by 97% (Henwood et al., 1992). Since 1992, TEDs also have been required in the winter trawl fishery for summer flounder operating as far north as Cape Charles, Virginia (Federal Register, 1992b).

* Contribution PRD-99/00-07 of the Southeast Fisheries Science Center, Miami, Florida 33149.

[1] STSSN (Sea Turtle Stranding and Salvage Network). 1998. Unpubl. data. The Sea Turtle Stranding and Salvage Network is a cooperative endeavor between NMFS, other federal agencies, the states, many academic and private entities, and innumerable volunteers. Data are archived at the National Marine Fisheries Service Southeast Fisheries Science Center, 75 Virginia Beach Dr., Miami, FL 33149.

[2] NMFS (National Marine Fisheries Service). 1990. Unpubl. data. NMFS Galveston Laboratory, 4700 Avenue U, Galveston, TX 77551.

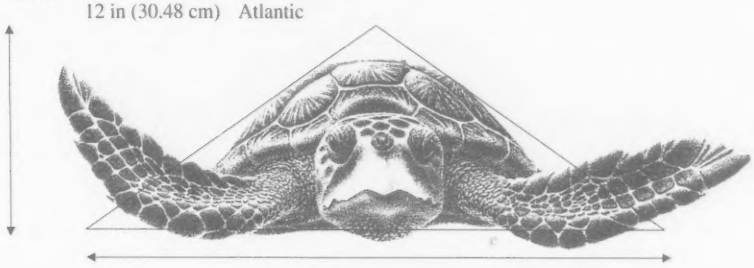

Figure 1

Minimum dimensions (height and width) specified in current U.S. federal regulations (Federal Register, 1992c) for escape openings in single-grid hard turtle excluder devices. The copyrighted figure of the turtle was kindly provided by Jamie Serino of Flying Turtle Productions.

TEDs are equipped with a trap door that allows sea turtles to escape from trawl nets (Seidel and McVea, 1982) and may be either rigid or soft in design (Federal Register, 1992c). To be certified by NMFS, a TED design must be 97% effective, in comparison with a control net, in excluding sea turtles (Federal Register 1987, 1992c). Since 1990, turtles used for TED trials have been small loggerhead turtles, mostly 2-yr-olds that have averaged 34.4 cm SCL (SD=4.1, n=1730, NMFS[3]). Regardless of design, certain parameters of the TED architecture are regulated. Most important to this discussion are the requirements of the height and width dimensions of the opening in the net through which turtles escape. Along the Atlantic Coast these requirements are width ≥35 in (88.90 cm) and height ≥12 in (30.48 cm) (Federal Register,1992c). In the Gulf of Mexico these measurements are ≥32 inch (81.28 cm) and ≥10 inch (25.40 cm), respectively. Height is measured simultaneously with width and is measured at the midpoint of the straight-line distance of width (i.e. the width and height of a taut triangle is measured, Fig. 1).

The purpose of our study was to compare the sizes of stranded sea turtles with the size of the TED openings. This evaluation was prompted by the need, identified by the NMFS Turtle Expert Working Group (TEWG), to reduce the strandings of mature loggerhead sea turtles (*Caretta caretta*) from the northern subpopulation (TEWG, 1998). We compared the sizes of stranded loggerhead, green (*Chelonia mydas*), and Kemp's ridley (*Lepidochelys kempii*) sea turtles, the three species most commonly found stranded, to the minimum widths and heights of TED openings.

[3] NMFS (National Marine Fisheries Service). 2001. Unpubl. data. Galveston Laboratory, National Marine Fisheries Service, 4700 Ave. U, Galveston, TX 77551.

Materials and methods

To compare the sizes of stranded turtles with the minimum size of TED openings we first constructed a predictor of carapace width and body depth. Thus, a morphometric analysis for each species was conducted, generally with data from reared, live captured, or nesting turtles and not with data from strandings. The predictive regression for carapace width was then applied to the strandings data when this measurement was not recorded for a given turtle; the predictive regression for body depth was applied to all turtles in the database because body depth was rarely measured at stranding sites. We then analyzed the entire strandings database to compare turtle sizes with the minimum size of TED openings.

Morphometric analyses

The species-specific relationship between both body depth and carapace width with carapace length was explored through regression analysis and predictive regression equations were developed. Regressions of untransformed data were compared with regressions of $\log_e$-transformed data by comparing goodness-of-fit values.

Morphometric data (straight line carapace length, notch-to-tip [SCL], straight line carapace width [SCW], and body depth [BD]) were recorded by a number of researchers throughout the southeast United States and at the Cayman Turtle Farm, Cayman Islands. Data for loggerhead turtles were concentrated in the 20–30 cm and 30–40 cm SCL size classes and were censored (randomized selection of n=37 in each of the two size classes) to create a more uniform distribution for the analysis (Table 1). Green turtle data were more uniformly distributed across size classes and were not censored (Table 1). Data for Kemp's ridley turtles were concentrated in the 1–10 cm and 10–20 cm

Table 1
Distribution of sizes of sea turtles used in the morphometric analysis.

Straight carapace length (cm)	Loggerhead		Green	Kemp's ridley	
	Frequency	Censored frequency	Frequency	Frequency	Censored frequency
1.01–10	1	1	17	3032	105
10.01–20	1	1	5	3778	105
20.01–30	123	37	37	155	155
30.01–40	629	37	49	58	58
40.01–50	24	24	22	137	137
50.01–60	48	48	21	71	71
60.01–70	26	26	16		
70.01–80	10	10	1		
80.01–90	32	32	3		
90.01–100	27	27	2		
100.01–120	7	7	3		

SCL size classes and were censored (randomized selection of n=105) in each of the two size classes (Table 1).

Strandings analyses

The Sea Turtle Stranding and Salvage Network (STSSN) documents dead or injured sea turtles along the coasts of the eastern United States and the U.S. Caribbean (Schroeder, 1989). The STSSN relies on a trained group of volunteers, including state and federal employees and private individuals, to collect basic biological data on each stranded turtle. Each animal is identified to species, the condition or state of decomposition is determined, standard carapace measurements are taken, and any obvious wounds, injuries, or abnormalities are noted and described. Volunteers who have received additional training may also perform necropsies, or internal exams, on a carcass to determine the general state of health of the animal prior to death, to determine sex, and to locate any obvious internal abnormalities. Data are recorded on standardized report forms that are submitted first to a state coordinator and then to the national STSSN coordinator at the National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, Florida.

The species-specific predictive regression equations from the morphometric analyses were used to estimate the carapace width for each turtle in the STSSN database for which this measurement had not been taken and to estimate the body depth for each turtle. For turtles with curved measurements only, straight line carapace lengths were estimated from curved carapace lengths (CCL) before estimating body depth and carapace width by applying equations reported by Teas (1993).

Within each region (Fig. 2) carapace widths were compared with the currently required minimum widths of TED openings and body depths were compared with the currently required minimum heights of TED openings. Stranded turtles that were reared in captivity, cold-stunned, or known to have been captured incidentally were censored.

Results

Morphometric analyses

Loggerhead sea turtles The relationships between carapace width and carapace length and between body depth and carapace length were linear. Coefficient of determination (r^2) values of regressions with $\log_e$-transformed data were slightly (<0.002) higher than values based on untransformed data. Regression of each of the morphometric values on carapace length was highly significant (P<0.0001) and resulted in the following predictive equations:

$$\ln SCW = -0.0225 + (0.9507 \times \ln SCL) \quad [n=250, r^2=0.989],$$

$$\ln BD = -0.5682 + (0.9100 \times \ln SCL) \quad [n=250, r^2=0.966].$$

Straight line carapace lengths corresponding to turtles with carapace widths of 81.28 cm (32 inch; the minimum width of TED openings in the Gulf of Mexico) and 88.90 cm (35 inch; the minimum width of TED openings in the Atlantic) were 104.5 cm and 114.9 cm, respectively. Straight line carapace lengths corresponding to turtles with body depths of 25.40 cm (10 inch is the minimum height of TED openings in the Gulf of Mexico) and 30.48 cm (12 inch is the minimum height of TED openings in the Atlantic) were 65.3 cm and 79.8 cm, respectively.

Green sea turtles The relationships between carapace width and carapace length and between body depth and

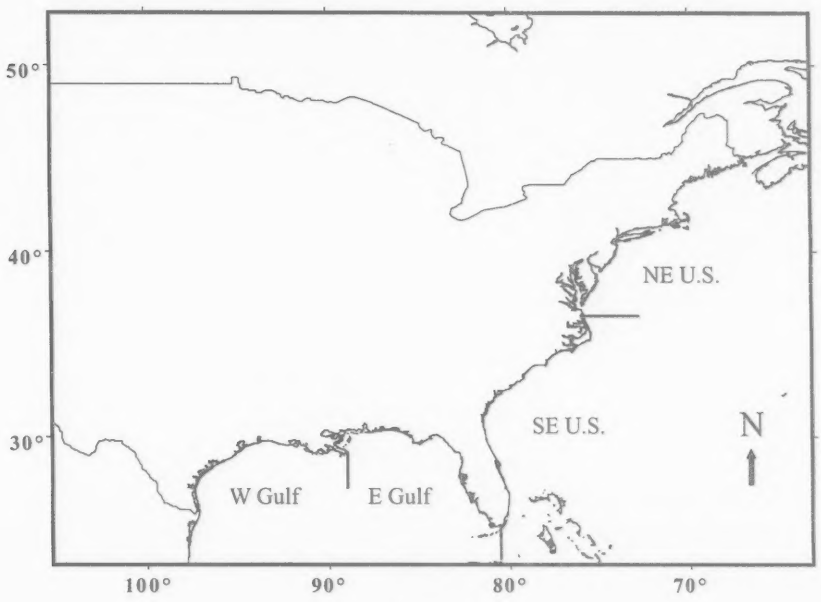

Figure 2

Regions of reported sea turtle strandings along the coasts of the eastern United States and the Gulf of Mexico.

carapace length were linear. Coefficient of determination (r^2) values of regressions with $\log_e$-transformed data were slightly (<0.015) higher than values based on untransformed data. Regression of each of the morphometrics on carapace length was highly significant (P<0.0001) and resulted in the following predictive equations:

$$\ln SCW = -0.1608 + (0.9812 \times \ln SCL), \quad [n=176, r^2=0.995],$$

$$\ln BD = -1.0115 + (1.0023 \times \ln SCL), \quad [n=176, r^2=0.977].$$

Straight line carapace lengths corresponding to turtles with carapace widths of 81.28 cm (32 inch) and 88.90 cm (35 inch) were 104.2 cm and 114.1 cm, respectively. Straight line carapace lengths corresponding to turtles with body depths of 25.40 cm (10 inch) and 30.48 cm (12 inch) were 69.2 cm and 83.0 cm, respectively.

Kemp's ridley sea turtles The relationships between carapace width and carapace length and between body depth and carapace length were linear. Coefficient of determination (r^2) values of regressions with $\log_e$-transformed data were slightly (<0.006) higher than values based on untransformed data. Regression of each of the morphometrics on carapace length was highly significant (P<0.0001) and resulted in the following predictive equations:

$$\ln SCW = -0.2039 + (1.0437 \times \ln SCL) \quad [n=631, r^2=0.998],$$

$$\ln BD = -0.6283 + (0.9075 \times \ln SCL), \quad [n=631, r^2=0.989].$$

Straight line carapace lengths corresponding to turtles with carapace widths of 81.28 cm (32 inch) and 88.90 cm (35 inch) were 82.2 cm and 89.6 cm, respectively. Straight line carapace lengths corresponding to turtles with body depths of 25.40 cm (10 inch) and 30.48 cm (12 inch) were 70.6 cm and 86.3 cm, respectively.

Strandings analyses

Straight carapace length and width were not measured for a number of stranded sea turtles; body depth almost never was recorded. The total number of records, by species, for which the predictive regressions were applied to estimate straight carapace length or straight carapace width are given in Table 2. Note that the length of a turtle, straight line or curved, must have been measured for the turtle to be included in the analyses because the predictive measures were based on length. It should also be noted that the conclusions from the strandings analyses were not altered by the choice of linear or log-transformed data in the morphometric analyses above.

Loggerhead sea turtles

Carapace width Strandings of loggerhead turtles with carapace widths greater than the currently required minimum widths of TED openings have not exceeded 1%

of the total measured strandings in any year since 1986 (Table 3). The majority of the stranded large (wide) turtles occur in the eastern Gulf of Mexico and the southeast U.S. Atlantic regions, areas where significant nesting occurs.

Body depth Strandings of loggerhead turtles with body depths greater than the currently required minimum heights of TED openings have ranged between 33% and 47% of the total stranded turtles measured every year since 1986 (Table 4). From 1995 to 1997 nearly 1300 stranded loggerhead turtles were deeper bodied that the currently required minimum TED height opening. The highest proportion of turtles that were too deep bodied to pass through TEDs was found to be in the Gulf of Mexico where TED openings are smaller. The greatest numbers of large turtle strandings occurred on nesting beaches of the eastern Gulf of Mexico and the southeast U.S. Atlantic.

Table 2

The total number of records, by species, for which the predictive regressions were applied to estimate straight line carapace length or straight line carapace width for loggerhead, green, and Kemp's ridley sea turtles.

Missing measurement	Loggerhead	Green	Kemp's ridley
Straight line carapace length	8340	1034	1209
Straight line carapace width	8555	1089	1261

Green sea turtles

Carapace width Strandings of green turtles with carapace widths greater than the currently required minimum width of TED openings have not exceeded two turtles or 2% of the total stranded turtles measured in any year since 1986 (Table 5).

Body depth Strandings of green turtles with body depths greater than the currently required minimum height of TED openings have ranged between 1% and 7% of the total stranded turtles measured since 1986 (Table 6). The large turtles were found sranded in the eastern Gulf of Mexico and the southeast U.S. Atlantic regions, the latter an area of nesting activity.

Kemp's ridley sea turtles

None of the nearly 3000 measured Kemp's ridley turtles that stranded during 1986–97 (total stranded=3476) had carapace widths or body depths greater than the currently required minimum widths and heights of TED openings.

Discussion

All ESA-listed species of sea turtles remain below their historic levels of abundance. The status of Kemp's ridley and loggerhead sea turtles was recently evaluated by the NMFS Turtle Expert Working Group (1998; 2000). Kemp's ridley turtles constitute a single management unit and the nesting population is increasing. If the population continues to grow exponentially, the recovery goal of downlisting

Table 3

Number of stranded loggerhead sea turtles and percentage of those measured with (predicted) carapace widths greater than the minimum width of openings currently required in turtle excluder devices.

	Region of stranding											
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number measured	Total number stranded
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%		
1986	0	0	2	2	5	1	1	5	8	1	959	1209
1987	1	1	3	2	5	1	0	0	9	1	1318	1728
1988	0	0	5	3	1	0	1	1	8	1	1105	1373
1989	0	0	3	1	1	4	0	0	7	1	1088	1425
1990	0	0	3	3	4	0	0	0	7	1	1258	1592
1991	0	0	2	2	1	0	0	0	3	0	777	975
1992	1	2	0	0	1	0	0	0	2	0	798	1101
1993	0	0	1	1	0	0	1	1	2	0	693	972
1994	0	0	5	7	2	0	0	0	7	1	1044	1342
1995	0	0	1	1	0	0	1	1	4	0	973	1424
1996	0	0	1	1	1	0	2	1	4	0	1461	1883
1997	0	0	6	4	0	0	2	1	8	1	1289	1643

the species from endangered to threatened status (10,000 females nesting in a season) will be met early in this century (TEWG, 2000). There are five known subpopulations of loggerhead turtles in the Western North Atlantic (Encalada et al., 1998; Francisco Pearce, 2001; Francisco et al., in press) but the status of only two could be addressed by the TEWG. Nesting levels of the South Florida subpopulation appear to be increasing, meeting one of the recovery goals set for Florida loggerhead sea turtles. The northern subpopulation, which nests from northern

Table 4

Number of stranded loggerhead sea turtles and percentage of those measured with predicted body depths greater than the minimum height of openings currently required in turtle excluder devices.

	Region of stranding										
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number measured
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	
1986	68	44	72	89	188	27	4	24	332	35	954
1987	75	54	123	96	225	23	11	25	434	33	1309
1988	62	56	134	96	187	25	6	17	389	38	1027
1989	41	44	209	92	179	26	4	19	433	42	1042
1990	48	36	91	88	250	27	6	22	395	33	1188
1991	37	54	73	83	162	31	18	30	290	40	734
1992	35	58	66	85	198	34	13	28	312	41	763
1993	26	47	76	89	182	40	12	28	296	47	636
1994	97	57	64	88	237	35	15	15	413	41	1010
1995	56	52	66	90	207	30	18	19	347	36	956
1996	99	52	127	88	253	27	33	20	512	36	1436
1997	97	66	131	87	171	23	29	14	428	34	1266

Table 5

Number of stranded green sea turtles and percentage of those measured with (predicted) carapace widths greater than the minimum width of openings currently required in turtle excluder devices.

	Region of stranding											
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number measured	Total number stranded
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%		
1986	0	0	2	22	0	0	0	0	2	2	101	125
1987	0	0	0	0	0	0	0	0	0	0	122	142
1988	0	0	0	0	0	0	0	0	0	0	178	193
1989	0	0	0	0	0	0	0	0	0	0	223	255
1990	0	0	0	0	0	0	0	0	0	0	280	308
1991	0	0	0	0	0	0	0	0	0	0	200	221
1992	0	0	1	4	0	0	0	0	1	1	184	208
1993	0	0	0	0	0	0	0	0	0	0	180	200
1994	0	0	0	0	0	0	0	0	0	0	268	320
1995	0	0	0	0	0	0	0	0	0	0	312	389
1996	0	0	0	0	1	0	0	0	1	0	508	584
1997	0	0	0	0	0	0	0	0	0	0	286	352

Table 6

Number of stranded green turtles and percentage of those measured with predicted body depths greater than the minimum height of openings currently required in turtle excluder devices.

	Region of stranding										
	Western Gulf		Eastern Gulf		SE U.S. Atlantic		NE U.S. Atlantic		All regions		Total number measured
Year	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	
1986	1	17	3	33	3	4	0	0	7	7	100
1987	2	13	3	12	3	4	0	0	8	7	122
1988	1	11	2	8	2	1	0	0	5	3	177
1989	3	21	3	9	6	3	0	0	12	5	219
1990	0	0	1	2	9	4	0	0	10	4	277
1991	0	0	3	8	3	2	0	0	6	3	196
1992	0	0	2	8	8	6	0	0	10	6	180
1993	0	0	4	11	4	3	1	33	9	5	175
1994	1	2	4	12	9	5	0	0	14	5	258
1995	0	0	1	2	3	1	0	0	4	1	301
1996	1	2	10	9	10	3	0	0	21	4	500
1997	1	3	4	10	7	3	0	0	12	4	282

Florida through North Carolina may now be stable but is currently well below goals set for its recovery (return to prelisting nesting levels). Mortality on at least the northern subpopulation of loggerhead sea turtles needs to be reduced throughout its range to ensure recovery.

Although subpopulations of loggerhead turtles can be easily distinguished by the geographic location of their nesting beaches, the subpopulations comingle on the foraging grounds (Sears, 1994; Norrgard, 1995; Sears et al., 1995; Rankin-Baransky et al., 2001; Witzell et al., 2002; Bass et al., in press). Genetic studies of foraging and stranded animals indicate that the immature benthic animals of the northern subpopulation are distributed along the Atlantic seaboard (Sears, 1994; Norrgard, 1995; Sears et al., 1995; Rankin-Baransky et al., 2001; Witzell et al., 2002; Bass et al., in press), in Florida Bay (Bass et al.[4]), and in the Gulf of Mexico (Bass et al.[5]). Non-nesting adult females from the northern subpopulation appear to occur exclusively along the east coast of the United States with rare exception, and none have been reported from international waters (Bell and Richardson, 1978; Williams and Frick, 2001; CMTTP[6]).

Eight nesting subpopulations were identified for green turtles in the Atlantic Ocean (Encalada et al., 1996), but later were reduced to five regional population units (Bass and Witzell, 2000). Like loggerheads, the subpopulations comingle on the foraging grounds (Bass et al., 1998; Lahanas et al., 1998; Bass and Witzell, 2000). The status of all these subpopulations has not been evaluated, but it appears that nesting levels are increasing on the east coast of Florida (Meylan et al., 1995; Florida Fish and Wildlife Conservation Commission[7]) as well as at Tortuguero, Costa Rica, the largest Western Atlantic rookery (Bjorndal et al., 1999).

A large proportion of stranded loggerhead turtles and a small proportion of stranded green turtles are too large to pass through the required minimum-sizes for TED openings. This finding is corroborated by analyses that suggest that the size distribution of stranded loggerheads is different (larger) than the size distribution of turtles in the nearshore waters (TEWG, 2000). The relatively large proportion of stranded loggerhead turtles with dimensions greater than the minimum height required for TED openings is cause for concern in light of the need to reduce mortality on the northern subpopulation of loggerhead sea

[4] Bass, A. L., M. Clinton, and B. W. Bowen. 1998. Loggerhead turtles (*Caretta caretta*) in Florida Bay: an assessment of origin based on genetic markers. Unpubl. report to Florida Department of Environmental Protection, 5 p. Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, 7922 NW 71st St., Gainesville, FL 32653.

[5] Bass, A. L., S.-M. Chow, and B. W. Bowen. 1999. Final report for project titled: genetic identities of loggerhead turtles stranded in the Southeast United States. Unpubl. report to National Marine Fisheries Service, order number 40AANF 809090, 11 p. Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st St., Gainesville, FL 32653.

[6] CMTTP (Cooperative Marine Turtle Tagging Program). 2001. Unpubl. data. The Cooperative Marine Turtle Tagging Program was established by NMFS in 1980 to centralize the tagging programs among sea turtle researchers, distribute tags, manage tagging data, and facilitate exchange of tag information. Since 1999 the CMTTP has been managed by the Archie Carr Center for Sea Turtle Research at the University of Florida, PO Box 118525, Gainesville, FL 32511.

[7] Florida Fish and Wildlife Conservation Commission. 2001. Unpubl. data. 100 Eighth Avenue S.E., St. Petersburg, FL 33701

turtles (TEWG, 1998; 2000) and indicates that, for loggerhead sea turtles, TEDs have not achieved a 97% reduction in captures by shrimp trawlers. Loggerhead turtles are exceeding in size the required minimum height of openings in TED before reaching maturity, especially in the Gulf of Mexico where the allowed opening is smaller than that in the Atlantic. This anomaly had not been noted previously because, since 1990, turtles used for TED trials have been small (<21 cm in body depth, n=1415; NMFS[3]). Based on stage elasticities, a proportional reduction in mortality in the smallest size classes not fitting through the TED openings (large immature turtles) would result in the greatest increased annual population multiplication rate (Crouse et al., 1987; Heppell, 1998a; Epperly et al., 2001). A reduction in subadult and adult mortality from drowning in trawls would benefit all species and subpopulations of sea turtles (Heppell, 1998b).

To decrease the mortality on large turtles caused by trawling, the opening dimensions of TEDs need to be larger than the current minimum requirements and need to be the same in the Gulf of Mexico and the Atlantic. Possible management options include the following: 1) increase the dimensions to accommodate some desired proportion of adults or the total population and 2) adopt the "leatherback" modification (Federal Register, 1993, 1994, 1995) for all areas and all times, which would allow the exclusion of turtles of all sizes, including leatherbacks which are the largest of the sea turtles. In response to our findings, an advance notice of a proposed rulemaking, to effect a change in TED requirements, was issued by NMFS (Federal Register, 2000). After consideration of public comments, NMFS advertised a proposed rule to change the TED requirements (Federal Register, 2001). NMFS should also consider extending the TED regulations to other bottom trawl fisheries of the Gulf of Mexico and along the Atlantic seaboard, including in the Northeast United States, whenever turtles and bottom trawling activity may co-occur.

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Habitat use by demersal nekton on the continental shelf in the Benguela ecosystem, southern Africa.

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Abstract—Videotapes collected by the research submersible *Jago* in the Benguela ecosystem during spring 1997 were analyzed to determine demersal nekton assemblage composition, fish behavior, and microscale habitat association, and habitat selection. Demersal fish assemblage diversity was generally low, and their composition was a function of substratum type. Individual species showed an often marked association with either rocky or soft substrata (or both), and a strong or weak selection for the associated biota. Soles and dragonets actively selected areas of bioactive soft substrata, to which they are behaviorally and morphologically adapted. False jacopever were associated with crevices in areas of high-relief rocky substrata. Kingklip are piscivorous and were largely confined to holes at the base of rocks and favored areas without a conspicuous epifauna. Juvenile hake and gobies avoided extremely rocky areas and were largely indifferent to the presence of benthic invertebrates—behavior that is consistent with their planktonic diets. These results represent the first direct observations of demersal nekton in the region and are important because they allow better interpretations of the results of trawl studies.

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The Benguela ecosystem is characterized by dynamic coastal upwelling (Shannon, 1985). It is among the most productive ecosystems in the world (Cushing, 1971) and supports several commercially valuable pelagic and demersal fisheries. Although we have a fairly good understanding of the role that the physical and biological environment play in influencing pelagic fishes (see references in Payne et al., 1987, 1992), the same cannot be said for the demersal species.

Although phytoplankton biomass and production in the Benguela ecosystem are high (Brown et al., 1991), there is a large mismatch with zooplankton (Hutchings, 1992) that results in significant sedimentation (Hutchings, 1992), and periodic anoxia on the bottom (Bailey and Rogers, 1997). Bottom currents are generally sluggish to the south (Shannon, 1985), and the seafloor is characterized by quartz sands, diatomaceous ooze, and foraminiferal deposits (Bailey and Rogers, 1997). Trawl studies have revealed that demersal fish diversity in the region is low and that assemblages can be subdivided into those inhabiting neritic, shelf, and slope areas (Macpherson and Roel, 1987; Roel, 1987; Macpherson and Gordoa, 1992; Smale et al., 1993). Correlations between demersal assemblages and the biophysical milieu (including landscape) have not been made owing to the general lack of environmental data, especially at the microscale.

Submersibles provide a way to sample and observe the biophysical environment of the sea floor. Although the method precludes an appreciation of the infauna, the technique allows for the simultaneous collection of information on the macroscopic benthic fauna and fishes, as well as on the physical features of the environment, across a wide variety of substrata. Elsewhere in the world, submersibles have been used to describe the physical and biological environment of benthic communities (Sibuet et al., 1988) to determine habitat use by nekton (Parker and Ross, 1986; Felley and Vecchione, 1995) and in data collection for stock assessment (Parker and Ross, 1986; Giguère and Brulotte, 1994).

During 1996, the research submersible *Jago* was used to examine some offshore areas near the mouth of the Orange River. A total of 17 dives were made and the archived videotapes were subjected to semiquantitative biological analysis (Gibbons et al., 2000). The *Jago* was commissioned again (by De Beers Marine [Pty.] Ltd.) in 1997 to collect a larger number of higher quality videotapes from the same area. In this article, we report on microscale habitat association and habitat selection by

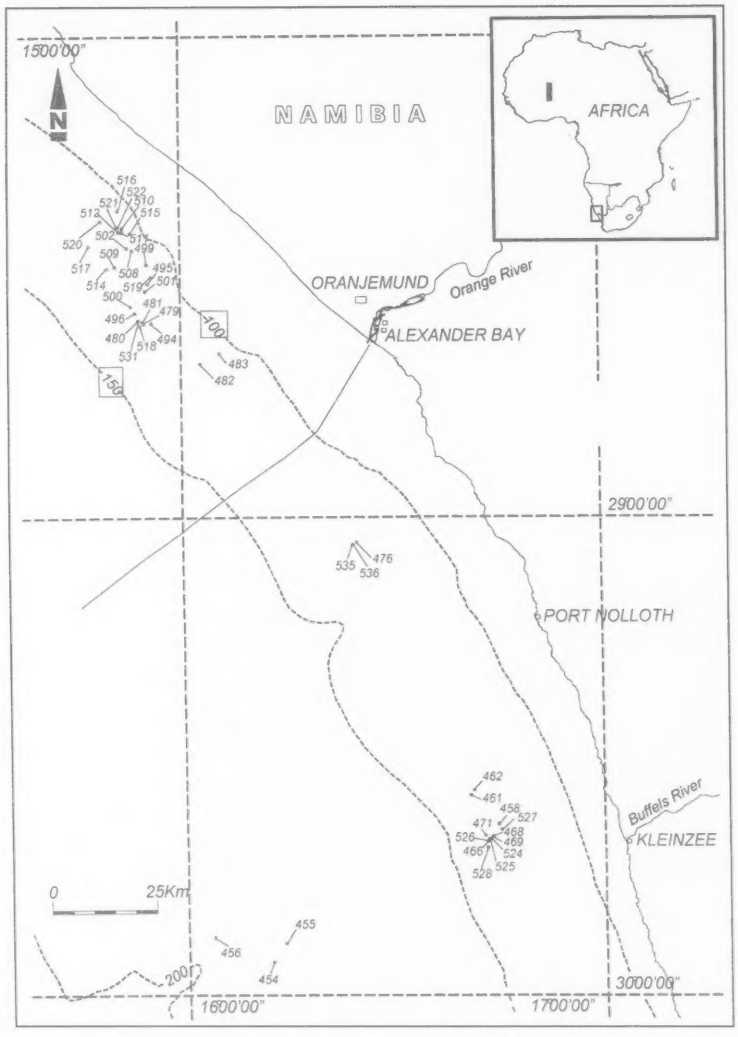

Figure 1

Map of the study area showing location of the dive sites and bathymetry. Numbers represent *Jago* dive numbers.

the common demersal nekton from these videotapes and examine fish behaviors and demersal fish assemblages.

Materials and methods

Field sampling

Videotapes of 44 diving sites in the Orange River delta area between 28°15′S and 29°40′S were analyzed. Surveys were conducted at depths between 100 and 140 m in the middle shelf (Fig. 1). Twenty-six dives were conducted north of the river mouth, and 18 were conducted to the south.

The submersible was launched from a support ship (MV *Zealous*) and towed by an inflatable dinghy to the first way-point of each dive survey. The position of the submersible was tracked every 31 seconds by using an acoustic transponder array. Accuracy of the positioning system was within approximately 5.0 m. A fairly detailed track-chart of the dive was produced and overlaid onto maps of underlying bathymetry.

Videotapes were recorded as the submersible cruised along the seabed (generally at speeds of 0.25 knots) by using a digital video camera. The camera usually faced forward and downward through the front acrylic dome-window and was only occasionally panned or moved during the survey. The submersible stopped at times, either so

Table 1

Distribution of number of samples (n) and area (m^2) in the different areas, among the major substratum types (by nature). Sand = soft sand, of variable texture and topography. With or without biogenic holes. Depth variable. Bioturbation maybe evident. Cobbles = fist-size rocks of claystone, sandstone, or quartzite. Of smooth and rounded appearance. Scattered or aggregated (sometimes densely) on sediment surface, and occasionally projecting through. With or without sediment layer or epifauna. Rock debris = smaller than boulders but larger than cobbles or gravel. Generally of irregular shape and not always smooth. Composed of sandstone or claystone. May project through, or sit on, sediment surface. Scattered or aggregated densely. With or without sediment on upper face. Epifauna maybe present. Boulders = massive, freestanding outcrops of rock, of high vertical relief, generally projecting through the sediment surface. Composed of either sandstone or claystone. Usually with some sediment on upper face. With or without encrusting fauna. Flat bedrock = slab-like sandstone or claystone rock of low vertical relief (<0.5 m), on sediment surface, usually with a thin sediment layer over upper surface. Epifauna on edges.

		North		South	
Major substratum	Substratum nature	n	Area	n	Area
Boulders	hard	3	61.53	1	12.41
Cobbles	hard	12	250.62	0	0
Cobbles	mixed	10	333.71	0	0
Rock debris	hard	40	1008.02	13	239.00
Flat bedrock	hard	9	199.86	0	0
Sand	mixed	97	3158.03	11	316.04
Sand	soft	80	2279.27	105	2123.85

that samples could be collected or to zoom in on particular features, and at other times it moved away from the bottom. Videotape recorded during these times, and when visibility was impaired due to silt disturbance, was not examined. The camera was rarely operated for the full duration of any one dive, and its use depended largely upon the interest of the geological observer. The video camera was equipped with a clock that was synchronized to that aboard the support vessel, so that it was possible to relate sections of the videotape to the actual position of the submersible on the dive-track. Illumination of the sea floor was provided by five 150-W halogen projectors arranged along a bar above the dome-window. A pair of red lasers (positioned 50 cm apart) were projected onto the sea floor to provide a moving scale.

Although the entire videotape from each dive was inspected, only samples of videotape were examined in detail and analyzed. The samples from each tape met the following criteria:

1 they were recorded along linear sections of the dive-track, as determined from the track-chart (to avoid looping and re-examination of previously sampled areas);
2 the submersible was moving at a slow (0.25 knots) but constant speed; and
3 there was no suspended sediment to impair visibility.

Samples were in multiples of selections that were 31 seconds in length. The bottom cover in each sample was first categorized by major (>50%) and subsidiary (>20%) substratum type (see descriptions in legend to Table 1), and then all sedentary biological features were recorded (as present or absent). A total of 381 samples was analyzed, most of which were in the northern area (Table 1). All nekton were identified and counted. Counts were subsequently converted to densities (m^2) with a knowledge of both the horizontal distance traversed by the *Jago* (calculated from the dive track with Autocad [Autodesk Inc., 1988]), and the width of the video-frame (calculated by using the distance between the two lasers, approx. 1–1.5 m).

Statistical analysis

Associations with environmental features The association between nekton and features of the physical and biological environment was examined by following Felley et al. (1989) and Felley and Vecchione (1995). In each sample, the primary substratum was given a score of 0.75, and the subsidiary substratum was allocated a score of 0.25: sedentary biological features were scored as either 1 (present) or 0 (absent). The mean environment was then calculated for each species, after weighting values of each of the environmental variables in each sample by density of individuals in that sample. Samples where no individuals were seen, made no contribution (since they had a weight of 0), whereas samples where the species was abundant made a marked contribution to the species mean. The mean for a variable reflected the relative state of that variable in samples where the species was most likely to be found, and can be thought of as its preference for that variable. A correlation matrix was then generated from all means for the measured environmental variables. Patterns of habitat use by species were reflected in patterns of interrelations among variables. Principal components analysis (PCA) was then performed on the correlation matrix. PCA resolves patterns of interrelationships among variables into a smaller set of composite variables (PCs) to which

observed variables (species abundances) were correlated. Each PC represents a particular trend in habitat use, and the axis differentiates among sets of species that are likely to be found in contrasting conditions for variables that define the PC. Because the PCs define axes, it is possible to plot species on these axes (using the PC scores) and thus identify those with contrasting or similar patterns of habitat use. Species with intermediate scores might be characteristic of intermediate environments, or they might be found over the entire range of environments reflected by a PC (because a species' score is the weighted mean of scores of samples where it was found). Habitat associations by demersal nekton were investigated separately from sites in the north and south because previous observations have suggested that areas to the north and south of the Orange River are distinct (Field et al., 1996).

Habitat selection by individual species can be determined by comparing species' variances on each PC with variance of the environment. Environmental variance on a PC was determined by calculating PC scores for each sample, following standardization with the appropriate mean of means, and standard deviation of means (see Felley and Vecchione, 1995). Then the scoring function was applied to each sample and the variance determined as the variance of sample scores. The score of each sample was assigned to each individual of all species seen in that sample. A species' variance was then calculated for each species as the variance of these scores. Levene's test was used to compare the species' variance with environmental variance. The null hypothesis invoked for these tests was "species" variance is not significantly different from environmental variance with respect to each factor." Active habitat selection by a species was inferred when a species variance was significantly smaller than the observed environmental variance (1-tailed test). This implies that the species was actively selecting a subset of the available environment with respect to that PC, i.e. species distribution in the study area was not random (see Felley et al., 1989). Comparisons of species variances with sample variances on each axis were performed only on the most common species, in each area because the sample sizes for most species were too small to allow statistically meaningful tests.

Assemblages Principal component analysis of the data revealed how species were distributed along composite environmental axes. Although species that are distributed in a similar way on a PC axis can be interpreted to share common responses to that axis, they do not necessarily occur together in the same assemblage. Alternative methods of analysis for examining species associations directly can be used to determine assemblage composition; as an alternative method, the software package PRIMER (Clarke and Warwick, 1994) was used in our study. With this software, descriptive, multivariate statistics allowed an examination of the relationships among the samples (based on similarities in specific composition of nekton) to determine how they were distributed with respect to the physical environment. Abundance of only those species that occurred in greater than 5% of the samples were root-root transformed, and a similarity matrix was constructed between the samples containing two or more species by using the Bray-Curtis index (Field et al., 1982). These matrices were used to plot classification diagrams of percentage similarity between samples by means of group-average sorting (fuller details of this method are provided by Field et al., 1996). Owing to the small area filmed in individual videotape samples (mean 26.20 m^2, SD 11.24 m^2), and the generally low density of most fish species, the samples were pooled (as in Dennis and Bright, 1988) by the nature of the substratum within a dive (hard, soft, mixed), so that replicates were of dives and not of individual videotape samples.

Activities In an effort to understand the behavior of demersal fishes in their natural environment, the activity of each demersal fish (on first sighting) was assigned to one of the following behavior patterns:

1 hovering off the substratum;
2 positioned on the substratum;
3 swimming in the water column;
4 positioned in a crevice or under an overhang;
5 occupying a shelter hole;
6 buried (fully or partially) in the substratum.

Observations of the substratum over which the fish was seen were also recorded, in the hope that it would be possible to correlate behaviors with the environment. The activity of each of the dominant species of demersal fishes was analyzed by using percent occurrence. This value was calculated by dividing the sum of all individuals observed in each activity (per major substratum type) by the total number of individuals of the species for which activities were recorded.

Results

Associations with environmental features

A total of 22 different taxa of demersal nekton were identified from the samples (Table 2). Eight of these were seen only once or twice, and only hakes occurred in more than 50% of the samples. The hakes were assumed to be *Merluccius capensis* on the basis of their inshore distribution (Roel, 1987). It was not always possible to clearly separate gobies, *Sufflogobius bibarbatus,* from dragonets, *Paracallionymus costatus*, and all cases of ambiguity were eliminated (i.e. only those fish that could be identified to species were included in the analyses).

Each species tended to be associated with slightly different features of the physical or biotic environment (or both).

North Eleven species were seen among these samples, and their mean environments are given in Table 3. PCA of the correlation matrix, generated from the mean environments of the six dominant species of nekton, produced three PCs with eigenvalues greater than one (Table 4). PC1 alone explained more than 60% of the variance in the

Table 2

Full list of all demersal nekton observed on the vidoetapes; * = observed once only.

Common name	Scientific name	Common name	Scientific name
Octopus	*Octopus vulgaris*	Kingklip	*Genypterus capensis*
Cuttlefish	*Sepia* spp.	Pelagic goby	*Sufflogobius bibarbatus*
Chokka squid	*Loligo vulgaris reynaudii*	Cape gurnard	*Chelidonichthys capensis*
Sixgill shark	*Hexanchus griseus**	West coast sole	*Austroglossus microlepis*
Smooth hound	*Mustelus mustelus**	Rough scale grenadier	*Caelorinchus simorhynchus*
Izak catshark	*Holohalaelurus regani*	Ladder dragonet	*Paracallionymus costatus*
St Joseph's shark	*Callorhinchus capensis**	Cape dory	*Zeus capensis**
Spearnose skate	*Raja alba**	Monk	*Lophius vomerinus**
Shallow-water Cape hake	*Merluccius capensis*	Cape conger eel	*Conger wilsoni**
False jacopever	*Sebastes capensis*	Snoek	*Thyrsites atun**
Jacopever	*Helicolenus dactylopterus*	Maasbanker	*Trachurus trachurus capensis*

data and contrasted species found over soft bioactive substrata (sole, *Austroglossus microlepis*, and to a lesser extent hakes) with those over more mixed and hard substrata (false jacopever, *Sebastes capensis*). The other species were located midway along this axis (Fig. 2).

PC2 accounted for almost 25% of the variance in the data set (Table 4). The significant loadings on the environmental variables essentially contrasted broken expanses of hard substrata (cobbles, and the biota associated with more open areas) with unbroken expanses of "lifeless" bedrock (Table 4). Those species that were previously contrasted along the PC1 axis were grouped together (false jacopever and sole) and set against those that were positioned midway between them (kingklip, *Genypterus capensis*, and goby) (Fig. 2).

PC3 was responsible for almost 10% of the variance in the data set (Table 4). It can be interpreted in terms of biological richness and contrasted gobies and soles with kingklip and hake (Table 4).

South A total of 10 species were seen in these samples, and their mean environments are given in Table 5. PCA of the correlation matrix generated from the dominant species' means produced four PCs with eigenvalues greater than one (Table 6). The first two PCs explained almost 75% of the variance in the data, although PC1 extracted only ~60%. A clear trend that differentiated the species was determined by PC1, which contrasted dragonets and soles with kingklip and false jacopever (Fig. 2). The loadings on the variables of PC1 (Table 6) opposed hard substrata and their associated epifauna at one extreme with sand and its associated organisms and structures at the other. PC2 contrasted gobies, kingklip, and hake with false jacopever and, to a lesser extent, jacopever, *Helicolenus dactylopterus* (Fig. 2). Interpretation of this PC is difficult because few

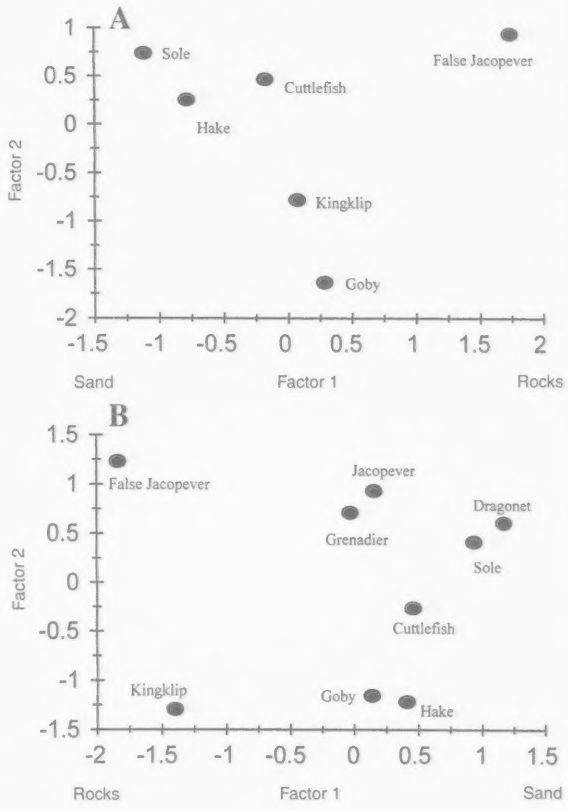

Figure 2

Distribution of species scores along the first and second axes representing habitat use by nekton species in the sites to the north (**A**) and south (**B**) of the Orange River mouth. PC1 (north and south) represented habitat use according to hard and soft substrata. PC2 (north) corresponded to the broken or continuous nature of the substratum, and PC2 (south) represented biological richness (see text).

Table 3

Species means for environmental variables in the undisturbed sites in the northern sampling area. Also given are the sample means total number of individuals of each species seen in samples (n). Data in bold typeface indicate those species used in the principal components

Species	Samples	Area	n	Sand	Cobbles	Debris	Boulders	Bedrock	Mounds
Hake	**177**	**5569.47**	**561**	**0.8266**	**0.0602**	**0.0971**	**0.0058**	**0.0102**	**0.9430**
False jacopever	**34**	**931.3**	**40**	**0.3750**	**0.1188**	**0.3750**	**0.0750**	**0.0563**	**0.7000**
Jacopever	1	18.93	1	0.2500	0	0	0	0.7500	1
Kingklip	**21**	**601.555**	**23**	**0.6087**	**0.0326**	**0.3261**	**0**	**0.0326**	**0.9565**
Goby	**21**	**604.98**	**25**	**0.5000**	**0.0300**	**0.3500**	**0**	**0.1200**	**0.8000**
Gurnard	4	88.2	4	0.8125	0	0.1875	0	0	1
Sole	**11**	**484.99**	**11**	**0.7727**	**0.1591**	**0.0682**	**0**	**0**	**1**
Grenadier	1	18.41	1	0	1	0	0	0	0
Dory	1	20.04	1	0.7500	0	0.2500	0	0	1
Octopus	4	94.86	4	0.6250	0.0625	0.3125	0	0	0.7500
Cuttlefish	**114**	**3721.355**	**183**	**0.7281**	**0.1011**	**0.1380**	**0.0041**	**0.0287**	**0.8852**
Environment	251	7291.03	251	0.6434	0.1116	0.1922	0.0149	0.0378	0.8207

Table 4

Eigenvalues generated from the principal components analysis (PCA) of the species means in the northern study site, using the dominant species only (Table 3). PC loadings of environmental means, and PC scores of the dominant species are also shown. The representations below are of the unrotated principle components. PC loadings greater than 0.50 are in bold typeface. FI, F2, F3 refer to factors 1–3, respectively, generated by the PCA.

	F1	F2	F3
Eigenvalue	9.14	3.481	1.40
% Total variance	60.95	23.21	9.33
Cumulative eigenvalue	9.14	12.62	14.02
Cumulative % variance	60.95	84.15	93.48
Sand	**–0.98**	0.18	0.11
Cobbles	0.34	**0.89**	–0.18
Rock Debris	**0.92**	–0.37	0.02
Boulders	**0.83**	0.49	–0.05
Bedrock	**0.53**	**–0.77**	–0.32
Mounds	**–0.92**	–0.10	0.21
Holes	**–0.83**	–0.47	0.07
Tracks	**–0.55**	–0.33	**–0.71**
Bryozoans	**0.93**	–0.25	0.20
Ascidians	**0.81**	–0.21	–0.51
Sponges	**0.94**	–0.10	–0.14
Cerianthids	**0.54**	**0.62**	0.15
Corals	**0.82**	**0.55**	–0.03
Asteroids	**–0.80**	**0.54**	–0.25
Hake	–0.79	0.26	0.92
False Jacopever	1.73	0.94	–0.20
Kingklip	0.07	–0.78	1.26
Goby	0.28	–1.63	–1.04
Sole	–1.12	0.74	–1.18
Cuttlefish	–0.18	0.47	0.23

of the environmental variables had significant loadings (Table 6); however, it would appear to reflect some level of biological richness.

PC3 accounted for 13% of the variance in the data set (Table 6), whereas PC4 was responsible for only 7%. The significant loadings on the environmental variables of the former contrasted the biota on hard substrata of high relief (boulder and reefs) with the biota of low relief areas (Table 6). PC4 contrasted (much of) the biota with the substrata, although few of the environmental variables had significant loadings (Table 6).

Selection of environmental features

The observed associations between nekton and the biophysical environment were often due to active selection. In the north only hake selected subsets of the available environment based on major substratum type (and its associated biota) (Table 7). This species avoided the rocky extremes, but otherwise showed a pattern of distribution that resembled that of the samples (Fig. 3A). Although false jacopever and hake selected opposite environments based on the broken or unbroken nature of the rock debris (PC2), it would appear that hakes again tended to avoid the extremes (Fig. 3, B and C). The other environmental PCs were not significantly selected for by any species.

Although interpretation of the results generated from the northern data set is confounded by the (mixed) nature of the samples (see Table 1), the same problems did not hamper the data from the south. In the south, six species of demersal nekton selected subsets of the available environment based on the identified axes (Table 7). Hake, goby, sole, and dragonet all appeared to select their environments on the basis of general physical features (PC1). As in the northern area, hake did not show a strong selection for axis extremes (e.g. Fig. 4A), which in itself could mean that hake did not favor very rocky or sandy areas. Dragonets and sole

for each variable, the total number of samples in which each species was seen, and the total area that these represented, as well as the analysis (PCA) (Table 4).

Holes	Tracks	Bryozoans	Ascidians	Sponges	Anemones	Cerianthids	Corals	Asteroids
0.9964	**0.0392**	**0.7023**	**0.3636**	**0.6720**	**0.4920**	**0.0089**	**0.0053**	**0.0784**
0.9000	**0**	**1**	**0.8000**	**0.9000**	**0.5000**	**0.0250**	**0.0500**	**0**
1	0	1	0	1	1	0	0	0
1	**0**	**0.9130**	**0.5652**	**0.7826**	**0.5652**	**0**	**0**	**0**
1	**0.0800**	**0.8800**	**0.7600**	**0.8000**	**0.5600**	**0**	**0**	**0**
1	0	0.7500	0	0.7500	0.7500	0	0	0
1	**0.0909**	**0.7273**	**0.6364**	**0.8182**	**0.2727**	**0**	**0**	**0.0909**
1	0	1	1	1	1	0	0	0
1	0	1	1	1	0	0	0	0
1	0	0.7500	0.5000	0.7500	0.2500	0	0	0
1	**0.0219**	**0.8033**	**0.5574**	**0.7596**	**0.4262**	**0.0219**	**0.0109**	**0.0601**
0.9482	0.0398	0.8048	0.5458	0.7610	0.5219	0.0120	0.0080	0.0478

showed distinct preferences for environments with sandy substrata (Fig. 4, B and C) and were absent from rockier areas. Dragonets and cuttlefish (*Sepia* sp.) appeared to select opposite environments along the PC2 axis, with the former favoring areas with echinoderms and sponges and the latter avoiding them. Hake again appeared to avoid extremes of environment along the PC3 axis, whereas false jacopever selected areas of high relief substrata (Fig. 4, D and E). The results suggest that hake selected areas without cerianthids (and other biota, PC4), whereas dragonet preferred areas with cerianthids (Table 7).

Assemblages

Assemblage composition was a function of substratum type. Cluster analysis of the similarity matrices generated between samples among all the data indicated a similarity in assemblage composition that was generally based on major substratum type (data not shown). These patterns were mirrored in separate analyses of the samples (Fig. 5, A and B). The communities were not always distinct, however, and samples from hard substrata were sometimes grouped with those from mixed, and even soft, substrata. A noteworthy feature of these data was the generally low level of similarity between samples, and this undoubtedly reflected their small individual size (area) and the low density of nekton.

The dendrogram produced by analysis of the species (and not sample) matrix revealed common patterns of association in both the northern and southern areas (Fig. 6, A and B). In the northern area, there were two clusters at the 30% level of similarity (with sole as an out-group) (Fig. 6A). This result is difficult to interpret clearly because the one group comprised species of both soft (hake and cuttlefish) and hard (false jacopever) substrata. These species were also the most abundant and thus the likelihood of their co-occurrence in samples was high. In the south, two groups of associated species were also observed at the 30% level of similarity. The association between hake and cuttlefish was again tight, and both were more distantly linked to false jacopever (Fig. 6B). The other group comprised two clusters at the 40% level of similarity: one of gobies and grenadiers, *Caelorinchus simorhynchus*, and the other of species from soft (dragonets and sole) and mixed substrata.

Activities

None of the dominant species appeared to be either attracted to, or repelled by, the presence of the submersible and its lights, and avoidance behavior was seen only at the moment when the submersible was directly over the fishes.

Few of the fishes seen were actually swimming (behavior pattern 3), and most were resting on the substratum itself (Fig. 7). Indeed, all gobies and soles were seen lying on the substratum. Grenadiers seemed to hover above the substratum, and false jacopever and kingklip appeared to be situated in some sort of shelter. Although a few individual hake, kingklip, and dragonets buried themselves in sand, this behavior was otherwise uncommon. Most of the fish seemed to behave in a similar way over hard and soft substrata. The exceptions to this were kingklip and grenadiers, which tended to hide and rest, respectively, more often over hard substrata rather than soft (Fig. 7).

Discussion

The demersal nekton assemblages over the continental shelf along the west coast of southern Africa are clearly structured in a way that reflects the substratum type. This assemblage composition is in part due to the responses of individual species to the environment. These are novel observations for the region, and they provide a baseline

Table 5

Species means for environmental variables in the undisturbed sites in the southern sampling area. Also given are the sample means total number of individuals of each species seen. Data in bold typeface indicate those used in the PCA (Table 6). T-worms = tube worms.

Species	Fish no.	Samples	Area	Sand	Debris	Boulders	Reefs	Mounds	Holes	Tracks
Hake	**580**	**110**	**2285.12**	**0.987**	**0.013**	**0**	**0**	**0.794**	**1**	**0.331**
False jacopever	**16**	**15**	**347.61**	**0.581**	**0.312**	**0.080**	**0.027**	**0.446**	**0.893**	**0.142**
Jacopever	**7**	**6**	**115.09**	**0.827**	**0.173**	**0**	**0**	**0.821**	**1**	**0.526**
Kingklip	**4**	**4**	**82.73**	**0.564**	**0.436**	**0**	**0**	**0.111**	**1**	**0**
Goby	**14**	**13**	**312.42**	**0.930**	**0.070**	**0**	**0**	**1**	**1**	**0.412**
Gurnard	4	3	67.00	0.901	0.099	0	0	0.250	1	0.250
Sole	**24**	**22**	**414.27**	**1**	**0**	**0**	**0**	**0.967**	**1**	**0.599**
Grenadier	**15**	**14**	**243.65**	**0.668**	**0.332**	**0**	**0**	**0.750**	**1**	**0.661**
Dragonet	**110**	**50**	**853.44**	**1**	**0**	**0**	**0**	**0.988**	**1**	**0.613**
Cuttlefish	**172**	**84**	**1814.90**	**0.935**	**0.061**	**0.004**	**0**	**0.828**	**1**	**0.355**
Environment	130	130	2691.29	0.868	0.118	0.012	0.003	0.717	0.981	0.400

Table 6

Eigenvalues generated from the PCA of the species means in the southern study site, using the dominant species only (Table 5). PC loadings of environmental means, and PC scores of the dominant species are also shown. The representations below are of the unrotated principle components. PC loadings greater than 0.50 are in bold typeface.

	F1	F2	F3	F4		F1	F2	F3	F4
Eigenvalue	10.11	2.56	2.27	1.11	Cerianthids	**0.52**	0.05	0.45	**0.65**
% Total variance	59.45	15.06	13.38	6.54	Corals	**–0.94**	0.24	–0.05	0.03
Cumulative eigenvalue	10.11	12.67	14.94	16.05	Asteroids	**0.72**	0.15	0.43	0.36
Cumulative % variance	59.45	74.50	87.88	94.42	Ophiuroids	0.29	**0.50**	**–0.65**	–0.30
Sand	**0.91**	–0.17	0.30	–0.19	Echinoids	**0.60**	**0.52**	–0.43	0.28
Rock Debris	**–0.85**	0.08	–0.44	0.24	Tube worms	**–0.90**	–0.36	–0.02	0.02
Boulders	**–0.68**	0.46	**0.54**	–0.16	Hake	0.41	–1.21	0.47	–0.63
Reefs	**–0.69**	0.46	**0.52**	–0.17	False jacopever	–1.84	1.23	1.40	–0.46
Mounds	**0.87**	0.17	0.16	–0.34	Jacopever	0.16	0.94	–1.41	–0.77
Holes	**0.69**	–0.46	**–0.52**	0.17	Kingklip	–1.40	–1.29	–0.83	1.24
Tracks	**0.80**	0.45	–0.24	–0.13	Goby	0.14	–1.15	0.27	–1.33
Bryozoans	**–0.99**	0.07	0.01	0.02	Sole	0.94	0.42	0.11	–0.70
Ascidians	**–0.94**	0.08	–0.24	0.21	Grenadier	–0.03	0.72	–1.42	0.30
Sponges	0.07	**0.96**	–0.10	0.20	Dragonet	1.17	0.61	0.84	1.48
Anemones	**–0.98**	–0.06	–0.14	0.00	Cuttlefish	0.46	–0.26	0.58	0.85

set of information that should allow a more meaningful interpretation of the results of the (more typical) trawl surveys for fishes.

Species accounts

False jacopever have been positively correlated with rocky areas from a previous study of the region (Gibbons et al., 2000). Members of the genus *Sebastes* are also known as rockfish and have been reported as common over deep rocky reefs from video-surveys (Richards, 1986; Murie et al., 1994). They seem to prefer structured and high-relief reefs, and a partitioning of the habitat has been observed among congeners (Richards, 1986). Rockfish have been reported as scarce over soft sediments (Stein et al., 1992). Our results are consistent with those from previous studies.

Jacopever was the other scorpionid fish observed in our study. It was far less common than false jacopever and appeared to have a markedly different association with environmental features. Admittedly the sample size for

for each variable, the total number of samples in which each species was seen and the total area that these represented, as well as the

Bryozoans	Ascidians	Sponges	Anemones	Cerianthids	Corals	Asteroids	Ophiuroids	Echinoids	T-worms
0.120	**0.022**	**0.701**	**0.189**	**0.011**	**0.028**	**0.085**	**0.018**	**0.062**	**0.345**
1	**0.668**	**1**	**0.784**	**0**	**0.641**	**0**	**0**	**0**	**0.511**
0.333	**0.333**	**1**	**0.333**	**0**	**0.333**	**0**	**0.209**	**0.138**	**0.155**
0.794	**0.794**	**0.794**	**0.794**	**0**	**0.474**	**0**	**0**	**0**	**0.570**
0.358	**0.094**	**0.745**	**0.390**	**0**	**0.094**	**0**	**0**	**0**	**0.306**
0.645	0.395	0.645	0.250	0	0.395	0	0	0	0.605
0	**0**	**0.979**	**0.030**	**0**	**0**	**0.220**	**0.095**	**0.094**	**0.084**
0.372	**0.333**	**1**	**0.413**	**0**	**0.162**	**0**	**0.080**	**0.203**	**0.331**
0.024	**0**	**1**	**0.024**	**0.053**	**0**	**0.277**	**0.021**	**0.161**	**0.012**
0.203	**0.115**	**0.900**	**0.158**	**0.041**	**0.130**	**0.125**	**0.022**	**0.093**	**0.271**
0.279	0.175	0.825	0.300	0.020	0.141	0.115	0.028	0.065	0.290

Table 7

Distribution tests of individuals of different species on principal components describing environmental use by dominant demersal fishes in the northern and southern study sites. Levene's test of variance equality was used to compare species' variances with variance of samples on each principal component. X and XX indicate a species' variance significantly smaller than location variance at the $P<0.10$ and $P<0.05$ level, respectively (implying that the species uses a subset of available conditions relative to that principal component).

Species	PC1	PC2	PC3	Species	PC1	PC2	PC3	PC4
Hake	XX	XX		Hake	XX		XX	XX
False jacopever		XX		False jacopever			X	
Kingklip				Goby	X			
Goby				Sole	XX			
Sole				Grenadier				
Cuttlefish				Dragonet	XX	XX		X
				Cuttlefish		XX		

jacopever was very small, but it showed a weaker association with high-relief hard substrata and a greater association with more open areas. *Helicolenus dactylopterus* is a conspicuous spcies in trawl catches in the region (Roel, 1987), unlike *S. capensis*, and the difference in habitat use would explain this. Both species are likely to be largely piscivorous as adults (Macpherson and Roel, 1987; Meyer and Smale, 1991), and therefore the association of *S. capensis* with a rich epifauna is more likely an artifact of autocorrelation with hard substrata (per se) than real.

Kingklip have also been correlated with rock cover (Gibbons et al., 2000). Although it is a bycatch species of the commercial trawl fishery over (presumably) mixed grounds (Payne, 1985), a high CPUE is achieved by using long-lines over hard grounds (Badenhorst, 1988). This high CPUE could imply that it is found at greater densities over hard grounds and that the species shows some sort of preference for rocky areas (as suggested by Japp, 1990). In his study of feeding patterns of kingklip, Macpherson (1983) suggested that it probably inhabited holes in the mud (or caves) during the daytime. Our observations indicated that this species hides in holes by day (Fig. 7C), but that these holes are generally at the base of rocks. Such a shelter provides them with ready access to their favored prey (demersal fishes) on the sandy areas surrounding (Macpherson, 1983; Macpherson and Roel, 1987) and would account for a lack of association with conspicuous mobile epifauna..

By contrast, sole have been observed by Stein et al. (1992) to favor areas of soft substrata and tend to be caught in greatest numbers there (Payne, 1985). Both sole and dragonets (Tables 4 and 6) certainly show morphological adaptations to this substratum type and are dorsoventrally flattened to a greater (sole) or lesser (dragonet) extent. These species were also associated with areas having

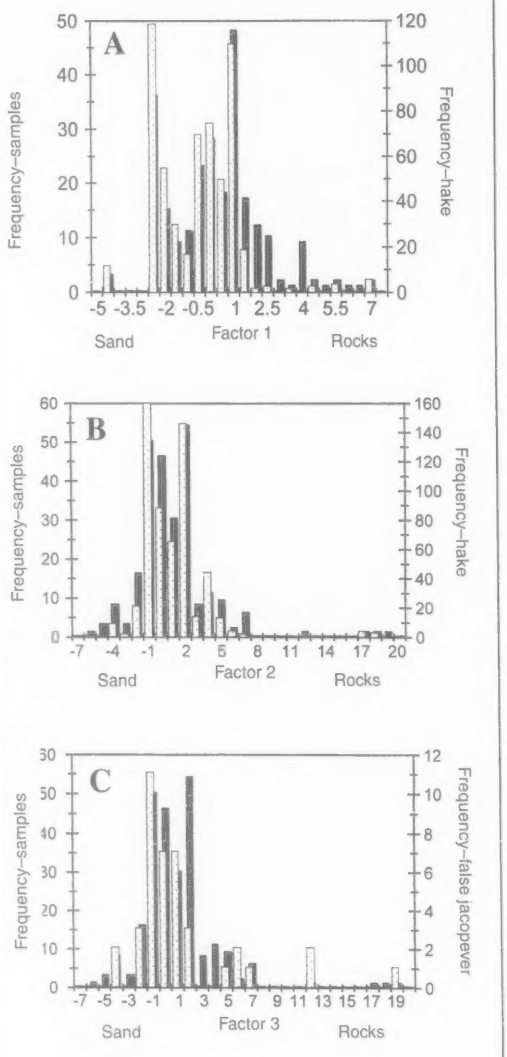

Figure 3

Distribution of hake (stippled), and samples (solid), on the principal components 1 (PC1) axis which represented hard and soft substrata, in the sites to the north of the Orange River mouth (**A**). Distribution of hake (**B**), and false jacopever (**C**) (both stippled) and samples (solid) on the PC2 axis which represented biotic richness, in the sites to the north of the Orange River mouth. The variance of all species scores was significantly less than that of sample scores.

a rich infauna (Table 4), which probably reflects the strictly benthic nature of their diets (Macpherson and Roel, 1987).

An apparent lack of strong habitat preference has been observed by longfin hakes (*Urophycis chesteri*) off North Carolina (Felley and Vecchione, 1995). Although similar results were noted here for *Merluccius capensis* (e.g. Tables 4 and 6), this species tended to avoid the rocky extremes (as in Gibbons et al., 2000). Interestingly, the species was not associated with substrata that were conspicuously rich in either epifauna or infauna. However, because small hake

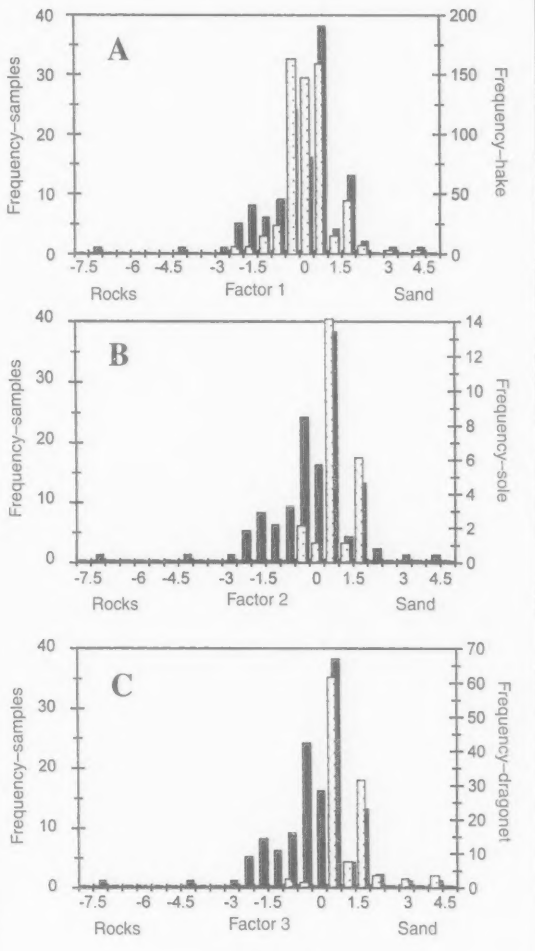

Figure 4

Distribution of hake (**A**), sole (**B**) and dragonet (**C**) (all stippled), and samples (solid) on the PC1 axis which represented hard and soft substrata, in the sites to the south of the Orange River mouth. Distribution of hake (**D**) and false jacopever (**E**)(both stippled), and samples (solid) on the PC3 axis which represented vertical structure, in the sites to the south of the Orange River mouth. The variance of all species scores was significantly less than that of sample scores.

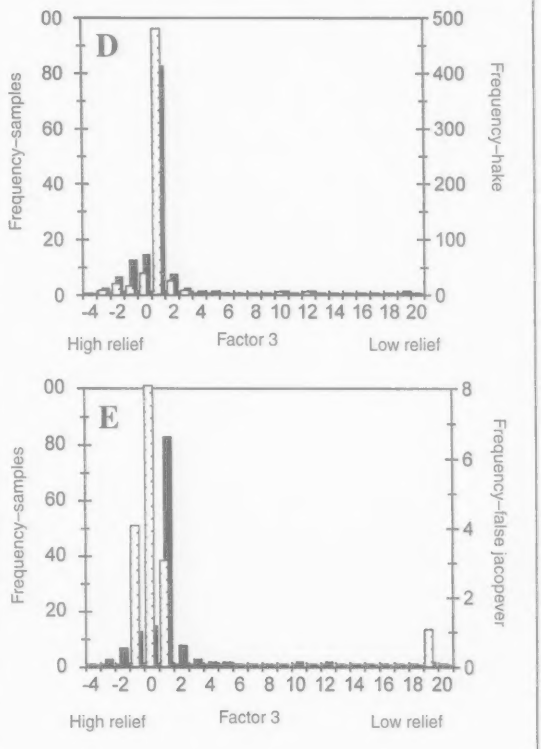

Figure 4 (continued)

display strong vertical migration at night and feed primarily on macrozooplankton (Pillar and Barange, 1995), a pronounced association with a benthic fauna need not be expected. Should the use of the demersal environment by hake during the day, therefore, simply be one of a place to rest, then the preference for sandy areas needs to be interpreted in terms of favored shelter. Our observations of hake behavior (Fig. 7A) indicated that most individuals were positioned immediately on the sand, although some were buried in the upper layers of the substratum. Under the white lights of the *Jago*, these juvenile hake were pink and blotchy in color and appearance and were not strongly different from kingklip, and it is possible that such an appearance may serve to camouflage individuals.

Cuttlefish are well known to use camouflage, and this may account for the fact that they were not strongly associated with soft or hard substrata (Tables 4 and 6). Cuttlefish are the commonest cephalopod caught in demersal trawls (Japp, 1997), implying that they are known to occur over sandy and mixed substrata. Cuttlefish feed predominantly on fishes and crustaceans (Lipinski, 1992) and therefore the lack of any strong association with ophiuroids is to be expected.

Grenadiers, on the other hand, tended to be associated with brittlestars (Table 6). Unlike cuttlefish, however, grenadiers are known to feed quite extensively on ophiuroids[1] and small epifauna (Meyer and Smale, 1991) and did not seem to show any strong association with extremes of substrata and were observed in both soft and hard habitats (Table 5). The smaller species of macruorids (such as *C. simorhynchus*) form a small but conspicuous part of the

[1] Adriaans, W. 2000. Unpubl. data. Zoology Department, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa.

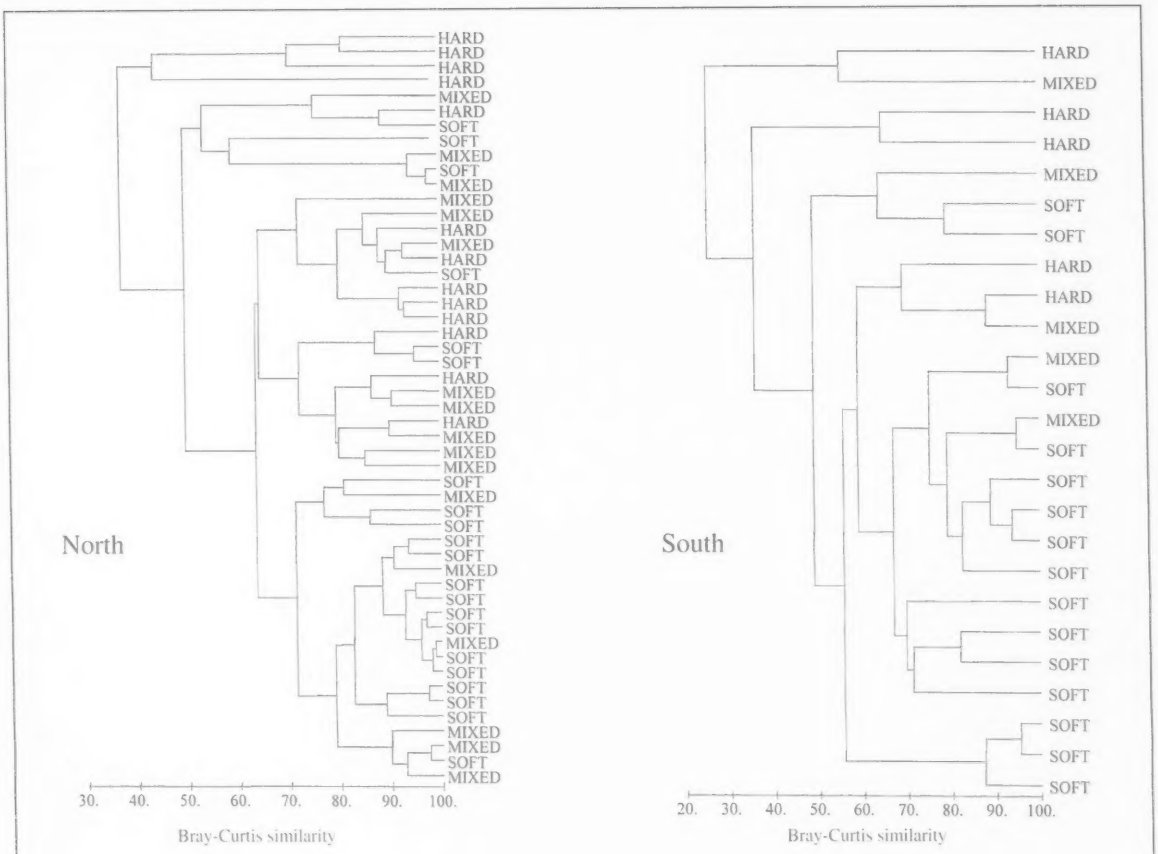

Figure 5

Cluster analysis of the pooled (by major substratum per dive) samples of nekton collected over the areas to the north and south of the Orange River mouth.

bycatch from the hake-directed trawl fishery and are thus assumed to occupy a wide range of habitats.

The gobies seen in our study tended to show neither a strong association with any substratum type (and their associated biota), nor were they linked to areas with a rich ophiuroid fauna (Tables 4 and 6). *Sufflogobius bibarbatus* is also known as the pelagic goby because it spends much of its time at night in the water column,[2] where it forms a conspicuous part of the fish community[3] and where it feeds largely on zooplankton.[2] If the gobies observed in our study were *S. bibarbatus* (as postulated), then the data suggest that their use of the demersal habitat by day was primarily linked to shelter. Otherwide, it might be expected that they would be associated with areas rich in benthic food, such as ophiuroids, which are known to form part of the diet of other gobies (Gibson, 1982).

Communities

The overall diversity of the fish community observed by the *Jago* is less than that determined from the same region with trawl nets (Roel, 1987), principally because the area sampled was significantly smaller. The diversity of the fish and cephalopod fauna may also seem low by comparison with submersible surveys elsewhere (e.g. Felley et al., 1989). But, this region is not known to support a high diversity of demersal species (Mas-Riera et al., 1990) because of the perceived harshness of the prevailing environment (such as frequent intrusions of low-oxygen bottom water (Bailey and Rogers, 1997)).

The demersal nekton fauna, both as individual species and as a whole, was strongly influenced by substratum type (as in Parker et al., 1994). Despite the large research effort

[2] Pillar, S. C. 2000. Personal commun. Marine and Coastal Management, Cape Town, South Africa.

[3] O'Toole, M. 2000. Personal commun. Ministry of Fisheries and Marine Resources, Windhoek, Namibia.

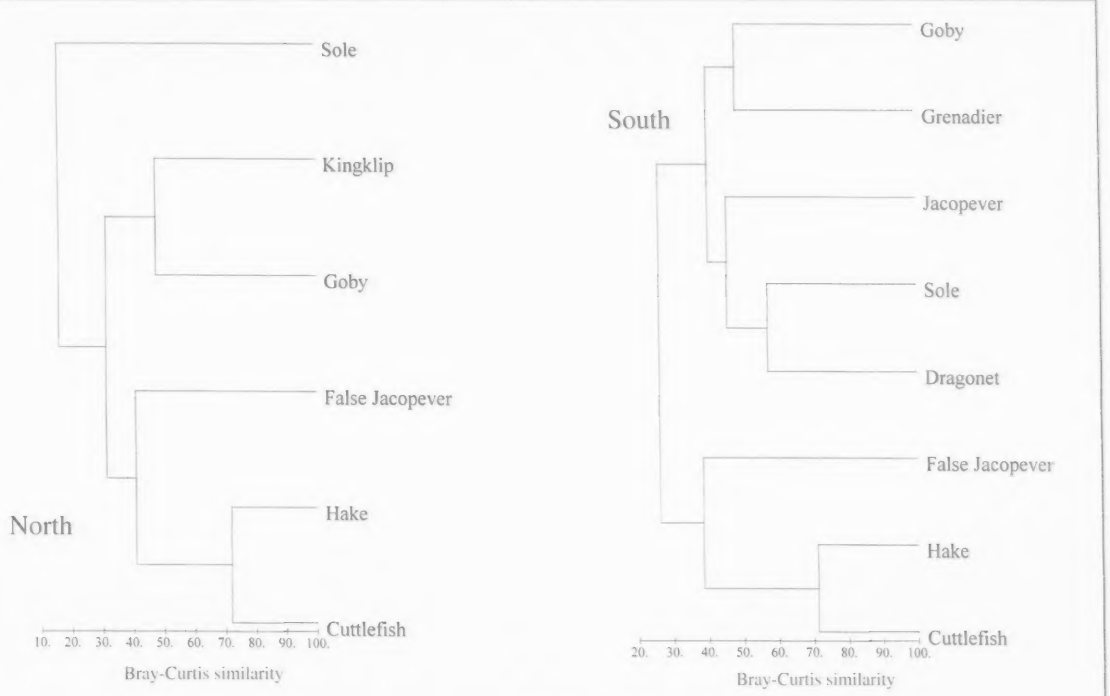

Figure 6

Inverse classification diagram showing species' associations among all the samples (pooled by major substratum and dive) collected in the sites to the north and south of the Orange River mouth.

that has focussed on the commercially important demersal fisheries along the west coast of southern Africa, there is a dearth of published material that can be usefully compared to the current observations. Roel (1987) recognized that the species composition of the demersal fauna in the southern Benguela ecosystem was mainly influenced by depth, and she identified two distinct communities of demersal nekton. One of these was dominated by *Merluccius paradoxus* and occurred at depths greater than 380 m, and the other was dominated by *M. capensis* and was confined to the continental shelf. In the northern Benguela ecosystem, Macpherson and Roel (1987) recognized five distinct demersal fish communities. Two of these were distributed over the shelf (and were subdivided by latitude), and the balance was essentially depth related and ran parallel to the coastline, offshore. Similar observations on the structure of the demersal fish assemblages were made by Macpherson and Gordoa (1992) and Mas-Riera et al. (1990), who noted that latitudinal variations in community composition were generally associated with the state of upwelling. The latter authors postulated that the especially low level of diversity of the demersal fish community in the northern Beguela ecosystem (the region of our study) was due to the presence of low-oxygen bottom water. The "indicator" species for the assemblage in their analysis included *Merluccius capensis* and *Sufflogobius bibarbatus*, which were also among the common species observed in our study.

Smale et al. (1993) observed three demersal communities over the Agulhas Bank (south coast of South Africa) which were related to depth; inshore (<100 m), shelf (90–190 m), and slope (>200 m). Although the species observed in the our surveys were all conspicuous components of the shelf communities identified by the these authors, they were relatively rare (or absent) from the samples collected by Smale et al. (1993). Unfortunately, the nature of these authors' data (30–60 minute trawls) is such that they do not provide any fine-scale information on species associations, and this effectively limits further comparison.

There appears to be a difference in the community of fishes from the northern and southern study sites (e.g. the presence of dragonets in the south but not in the north). Differences in the infaunal communities from undisturbed sites to the north and south of the Orange River were noted by Field et al. (1996). Gibbons and Sulaiman[4]

[4] Gibbons, M. J., and A. Sulaiman. 1998. A video-description of the mid-shelf benthic environment off the west coast of southern Africa, with a comment on the habitat association of demersal nekton. A report to De Beers Marine (Pty) Ltd., Cape Town 8000, Republic of South Africa, 62 p.

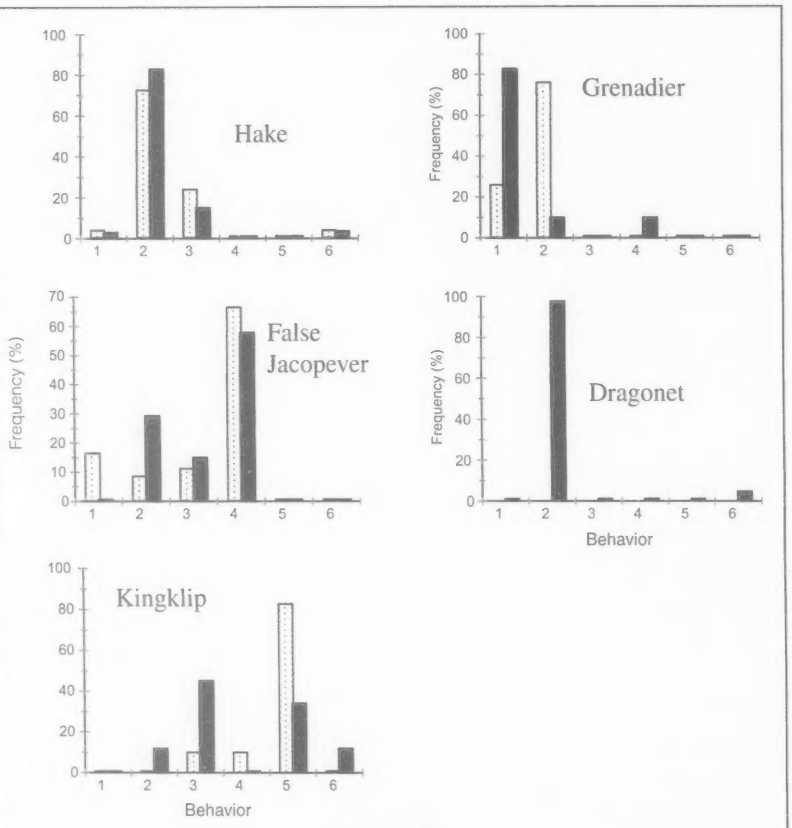

Figure 7

Histograms showing the frequency (as percent) at which behavior patterns 1–6 were observed (x-axis) in species videotaped during survey dives between 100–140 m in the Orange River delta area, southern Africa. All data were pooled. Behavior patterns: 1 = hovering off the substratum; 2 = positioned on the substratum; 3 = swimming in the water column; 4 = positioned in a crevice or under an overhang; 5 = occupying a shelter hole; 6 = buried (fully or partially) in the substratum. Solid bars indicate behaviors over soft substrata, stippled bars indicate behaviors over hard substrata.

also commented on some discrepancies in the structure of the physical and biological environment in regions to the north and south of the Orange River, which can be partly explained by the latitudinal influence of the River and by biogeography (Emanuel et al., 1992; Gibbons and Hutchings, 1996).

Acknowledgments

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Population structure of king mackerel (*Scomberomorus cavalla*) around peninsular Florida, as revealed by microsatellite DNA*

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Abstract—A total of 1006 king mackerel (*Scomberomorus cavalla*) representing 20 discrete samples collected between 1996 and 1998 along the east (Atlantic) and west (Gulf) coasts of Florida and the Florida Keys were assayed for allelic variation at seven nuclear-encoded microsatellites. No significant deviations from Hardy-Weinberg equilibrium expectations were found for six of the microsatellites, and genotypes at all microsatellites were independent. Allele distributions at each microsatellite were independent of sex and age of individuals. Homogeneity tests of spatial distributions of alleles at the microsatellites revealed two weakly divergent "genetic" subpopulations or stocks of king mackerel in Florida waters—one along the Atlantic coast and one along the Gulf coast. Homogeneity tests of allele distributions when samples were pooled along seasonal (temporal) boundaries, consistent with the temporal boundaries used currently for stock assessment and allocation of the king mackerel resource, were nonsignificant. The degree of genetic divergence between the two "genetic" stocks was small: on average, only 0.19% of the total genetic variance across all samples assayed occurred between the two regions. Cluster analysis, assignment tests, and spatial autocorrelation analysis did not generate patterns that were consistent with either geographic or spatial-temporal boundaries. King mackerel sampled from the Florida Keys could not be assigned unequivocally to either "genetic" stock. The genetic data were not consistent with current spatial-temporal boundaries employed in stock assessment and allocation of the king mackerel resource. The genetic differences between king mackerel in the Atlantic versus those in the Gulf most likely stem from reduced gene flow (migration) between the Atlantic and Gulf in relation to gene flow (migration) along the Atlantic and Gulf coasts of peninsular Florida. This difference is consistent with findings for other marine fishes where data indicate that the southern Florida peninsula serves (or has served) as a biogeographic boundary.

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The king mackerel (*Scomberomorus cavalla*) is a coastal pelagic fish distributed in the western Atlantic Ocean from Massachusetts (USA) to Rio de Janeiro (Brazil) and in the Gulf of Mexico and Caribbean Sea (Rivas, 1951; Collette and Nauen, 1983). Recreational and commercial catches of king mackerel in U.S. waters are substantial (Manooch, 1979; MSAP[1]; Legault et al.[2]) and the species is critical to the southeastern Atlantic coast (hereafter "Atlantic") and northern Gulf of Mexico (hereafter "Gulf") charter-boat industries. Management of the king mackerel resource in U.S. waters is under the jurisdiction of two regional fishery management councils, and current management planning (GMFMC[3]) is based on a two migratory unit (stock) hypothesis: one stock (Atlantic migratory unit) occurs in the U.S. southeastern Atlantic, the other (Gulf of Mexico migratory unit) occurs in the Gulf. Separation of the two stocks has been based primarily on mark-and-recapture studies carried out prior to 1984 and on differences in growth rate (MSAP[1]; Williams and Godcharles[4]). Based on the mark-and-recapture studies, it was hypothesized that the two stocks mixed extensively during

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[1] MSAP (Mackerel Stock Assessment Panel). 1994. Contribution report of the mackerel stock assessment panel. Contribution report MIA-93/94-42, 27 p. Southeast Fishery Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

[2] Legault, C. M., M. Ortiz, G. Scott, N. Cummings, and P. Phares. 2000. Stock assessment analyses on Gulf of Mexico king mackerel. Contribution report SFD-99/00-83, 48 p. Southeast Fishery Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

[3] GMFMC (Gulf of Mexico Fishery Management Council). 1996. Amendment 8 to the fishery management plan for coastal migratory pelagic resources in the Gulf of Mexico and South Atlantic includes environmental assessment, regulatory impact review, and initial regulatory flexibility analysis. Gulf of Mexico Fishery Management Council, 3018 U.S. Hwy, 301 North, Suite 1000, Tampa, FL 33619-2266.

[4] Williams, R. O., and M. F. Godcharles. 1984. Completion report, king mackerel tagging and stock assessment. Project rep. 2-341-R, plus figures and tables., 45 p. FL Dept. Nat. Res., Florida Marine Research Institute, 100 8th Ave. SE, St. Petersburg, FL 33701.

the winter months along the southeast coast of Florida. For purposes of stock assessment and resource allocation (Sutter et al., 1991; GMFMC[5]), the boundary between the two stocks was specified as the Volusia/Flagler county line (east coast of Florida) in winter (1 November–31 March) and the Monroe/Collier county line (west coast of Florida) in summer (1 April–31 October). Pragmatically, this means that king mackerel caught south of the Volusia/Flagler county line (including the Florida Keys) between 1 November and 31 March belong to Gulf stock, whereas fish caught south of the Monroe/Collier county line between 1 April and 31 October belong to Atlantic stock.

Data from additional mark-capture (Fable et al., 1987; Sutter et al., 1991; Schaefer and Fable, 1994; Fable[6]), growth rate (DeVries and Grimes, 1997), otolith shape (DeVries et al., 2002), and temporal-geographic sampling studies (Collins and Stender, 1987; Trent et al., 1983; Grimes et al., 1990) are consistent with the hypothesis that king mackerel in the Atlantic differ from those in the Gulf. In addition, on the basis of allozyme evidence (Johnson et al., 1993) and studies of early life history (Grimes et al., 1990; Grimes et al.[7]), DeVries and Grimes (1997) suggested that there might be two distinct stocks of king mackerel in the northern Gulf. Johnson et al. (1993) found a high frequency of the *PEPA-2a* allele of the nuclear-encoded dipeptidase (*PEPA-2*) locus among king mackerel from the western and northwestern Gulf, whereas a high frequency of the *PEPA-2b* allele occurred among king mackerel from the Atlantic and northeastern Gulf. Johnson et al. (1993) hypothesized that the two (putative) Gulf stocks mixed to varying degrees in the northern Gulf. Considering all the data acquired to date, DeVries and Grimes (1997) suggested there may be three stocks of king mackerel in U.S. waters: one in the Atlantic, one in the eastern Gulf, and one in the western Gulf.

The allozyme data of Johnson et al. (1993) did not distinguish king mackerel in the eastern Gulf from those in the Atlantic, and to that extent, argued against the hypothesis that king mackerel in the Atlantic and Gulf represented two distinct stocks. Gold et al. (1997), however, assayed variation in restriction sites of mitochondrial (mt)DNA among king mackerel collected from 13 localities along the U.S. Atlantic coast and northern Gulf and found significant (but weak) heterogeneity only in comparisons of pooled mtDNA haplotypes from Atlantic localities with pooled haplotypes from Gulf localities. Thus, the mtDNA data did not support the hypothesis that two genetically identifiable stocks of king mackerel occur in the northern Gulf, but rather were consistent with the hypothesis that separate stocks of king mackerel may exist in the Atlantic and in the Gulf. Estimates of F_{ST}, a measure of population subdivision, between king mackerel in the Atlantic and Gulf were small, indicating that mixing between Atlantic and Gulf king mackerel occurs.

Gold et al. (1997) also examined spatial variation in frequencies of the two alleles at *PEPA-2*. Results were essentially the same as those reported by Johnson et al. (1993): high frequency of the *PEPA-2a* allele among king mackerel in the western Gulf and high frequency of the *PEPA-2b* allele in the eastern Gulf and Atlantic. Tests of independence of *PEPA-2* genotypes with age and sex of individual fish, however, revealed significant nonrandom associations among Gulf fish of *PEPA-2a* homozygous genotypes with males and of *PEPA-2b* homozygous genotypes with females. Moreover, among fish sampled from the Atlantic, there was a highly significant decrease in the frequency of *PEPA-2b* alleles with increasing fish age. The same trend was found among fish sampled from the Gulf, but to a lesser extent. Tests of independence of sex versus age, and of mtDNA variation versus sex or age, were nonsignificant. These findings strongly indicated that the use of *PEPA-2* genotypes to distinguish stocks of king mackerel is compromised and that the hypothesis of eastern and western stocks of king mackerel in the Gulf needs to be re-evaluated.

Finally, Broughton et al. (2002) surveyed allelic variation at five nuclear-encoded microsatellites among a subset of the samples of king mackerel studied by Gold et al. (1997). Tests of homogeneity in allele distribution at the five microsatellites indicated that samples from Port Aransas, Texas (western Gulf), and Gulfport, Mississippi (central Gulf), differed from each other and from the remaining samples (including two samples from the Atlantic, one from the Florida Keys, one from the eastern Gulf, one from the western Gulf, and one from Veracruz, Mexico). No significant differences in allele frequencies at any microsatellite were found between samples representing geographic extremes, and no significant geographic patterns were found when samples were combined into regional groupings reflecting current hypotheses of king mackerel stock structure in U.S. waters.

Of concern to management of the king mackerel resource in U.S. waters is the degree of mixing between the presumed stocks in the Atlantic and Gulf. Analysis of mark-and-recapture data collected from 1985 to 1993 (MSAP[1]) indicated that roughly 3.0% of fish tagged in the Atlantic were recaptured in the Gulf, whereas 6.4% tagged in the Gulf were recovered in the Atlantic. More liberal estimates (SFC[8]) of recaptures (generated when utilizing summer

[5] GMFMC (Gulf of Mexico Fishery Management Council). 1984. Final amendment 1, fishery management plan and environmental impact statement for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. Gulf of Mexico Fishery Management Council, 3018 U.S. Hwy, 301 North, Suite 1000, Tampa, FL 33619-2266.

[6] Fable, W. A., Jr. 1988. Stock identification of king mackerel based on mark-recapture. Unpubl. manuscript from meeting on stock identification of king mackerel in the Gulf of Mexico. Southeast Fish. Sci. Center Contribution Report 2-18-88, 24 p. Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, FL 32408.

[7] Grimes, C. B., J. H. Finucane, and L. A. Collins. 1988. Distribution and occurrence of young king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico. Unpubl. manuscript from meeting on stock identification of king mackerel in the Gulf of Mexico. Panama City Lab. Contribution Report 2-18-88, 31 p. NMFS SE Fish. Cntr., 3500 Delwood Beach Road Panama City, FL 32408.

[8] SFC (Southeastern Fisheries Center). 1992. Preliminary analysis of southeastern U.S. king mackerel mark-recapture data: 1985–1993. Contribution report MIA-93/94-36, 19 p. Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL 33149.

and winter seasons in the "mixing" zone) suggested that 2.6–30.9% of recaptured tagged-fish in the Atlantic were returned as Gulf fish and 1.5–13.6% of recaptures tagged in the Gulf were returned as Atlantic fish. These mixing rates, however, were questioned (Jones et al.[9]) because virtual population analysis (VPA) based estimates of fishing mortality for the directed king mackerel fisheries in the Gulf and Atlantic corresponded to annual exploitation rates of 0.30 and 0.11, respectively, whereas exploitation rates calculated from the 1985–93 (uncorrected) tag returns ranged from 0.027 to 0.033 (Gulf) and from 0.036 to 0.045 (Atlantic). The difference between the two estimates of exploitation rates implied either that the true exploitation rate was overestimated by VPA or underestimated by uncorrected tag-return data, leading to the conclusion (Jones et al.[9]) that little confidence should be placed in reported mixing rates based on mark-and-recapture data.

The goals of this project were to use nuclear-encoded microsatellites to define more rigorously the spatial-temporal limits of the two stocks (if separate stocks exist) and to estimate the proportions of both stocks in the mixing zone. The issues of spatial-temporal limits and mixing of the two (presumed) stocks are important in relation to assessing and allocating the king mackerel resource, particularly during the winter season. For example, mark-recapture data (MSAP[1]) indicated that ~20% of fish tagged in the mixing zone in southeastern Florida moved into the Gulf. If this means that only ~20% of winter catches from the east coast of Florida are Gulf stock, as opposed to 100% under the current management plan, the allowable biological catch (ABC) for the Gulf stock would decrease significantly (MSAP[1]). Because the Gulf stock of king mackerel currently is considered overfished (Legault et al.[2]) reductions in ABC of the Gulf stock could have significant economic impact.

The choice to employ microsatellites for the project was straightforward. Briefly, microsatellites are rapidly evolving, short stretches of DNA composed of di-, tri-, and tetranucleotide arrays that are abundant, highly polymorphic, and inherited in a codominant fashion (Weber, 1990; Wright, 1993; Wright and Bentzen, 1994). Because allele frequencies at microsatellites are generally consistent with equilibrium expectations of diploid, Mendelian loci and because identification of individual microsatellites is by polymerase-chain-reaction (PCR) amplification, both of which remove most of the problems associated with homology of alleles, microsatellites have proven to be useful genetic markers of population structure in numerous taxa, including fishes (Angers and Bernatchez, 1998; Ruzzante et al., 1996; O'Connell et al., 1998; Nielsen et al., 1999). In addition, new alleles at microsatellite loci appear to arise rapidly (Schug et al., 1998), generating high allelic diversity important for statistical power in exact tests and other tests of allele-distribution homogeneity (Estoup et al., 1998; Ross et al., 1999).

[9] Jones, C. M., M. E. Chittenden, and J. R. Gold. 1994. Report to the mackerel stock identification working group. Unpubl. document of meeting held 8 Sep 94 to 9 Sep 94 at Panama City Lab., SE Fish. Sci. Cent. 7 p. Southeast Fisheries Science Center, National Marine Fisheries Service, 3500 Delwood Beach Road, Panama City, FL 32408.

Materials and methods

A total of 20 samples of king mackerel were procured between 1996 and 1998 from 11 different offshore sites (Table 1, Fig. 1). The sample from Panama City was obtained from charter boat catches, and the samples from Sarasota and Jacksonville were obtained from tournaments. The remaining samples were obtained from commercial catches. Tissue samples (heart and muscle) were removed from each fish, frozen in liquid nitrogen, transported to College Station, and stored at –80°C. Sex of individuals was recorded for all samples, except for the March 1997 sample from the Florida Keys. Approximate ages of individuals from all samples except for the July 1998 sample from Jacksonville, the March 1997 sample from the Florida Keys, and the April 1997 sample from Sarasota, were determined by otolith-increment analysis by following methods outlined in DeVries and Grimes (1997).

Initially, we planned to deploy the five microsatellites developed in a prior study (Broughton et al., 2002). Two of these (*Sca-8* and *Sca-47*), however, had proven difficult to amplify consistently in the prior study and therefore were omitted from our study. A third microsatellite, *Sca-30*, developed by Broughton et al. (2002), also was omitted because of difficulties with consistent amplification and because allele distributions at *Sca-30* were highly leptokurtic (Broughton et al., 2002). A total of five new microsatellites was then developed from the microsatellite-enriched genomic library generated by Broughton et al. (2002). Candidate microsatellites were sequenced from either or both ends by using standard M13 sequencing primers and an Applied Biosystems (Perkin Elmer) 377 automated DNA sequencer. The OLIGO software package (National Biosciences, Inc., 1992) was used to identify primers from regions flanking microsatellites. Primers were designed according to preset criteria that included product length, internal stability, proportion GC content, and primer Tm difference. PCR amplifications were performed under a variety of experimental conditions to optimize procedures that produced high yields of target sequence and minimized additional fragments ("stutter" bands). Experimental tractability (reproducibility, consistency, range in allele size, frequency of "stutter" bands [if present], and microsatellite polymorphism) of PCR-amplified microsatellites were evaluated by screening a panel of king mackerel samples available in the laboratory. PCR primer sequences, the length (in base pairs) of the cloned allele, and the annealing temperature in PCR amplification for the seven microsatellites used in the project are given in Appendix Table 1. Two of these, *Sca-37* and *Sca-44*, were developed previously by Broughton et al. (2002).

For assay of individual fish, genomic DNA was isolated from frozen tissues as described in Gold and Richardson (1991). Genotypes at the seven microsatellites were determined by PCR amplification and gel electrophoresis. Prior

Table 1

Localities, acronyms, dates of collection, and number of individuals (by sex) of king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys.

Sample locality	Acronym	Date of capture	Number of individuals			Migratory group[1]
			Female	Male	Total	
Atlantic Ocean (east coast)						
Jacksonville, FL	JCK[1]	Jul 1996	48	0	48	Atlantic
Jacksonville, FL	JCK[2]	Jul 1998	28	3	31	Atlantic
New Smryna Beach, FL	NSB	Jul 1996	41	9	50	Atlantic
Cape Canaveral, FL	CCN	Dec 1998	24	26	50	Gulf
Sebastian, FL	SEB[1]	Mar 1997	29	21	50	Gulf
Sebastian, FL	SEB[2]	Mar 1998	24	26	50	Gulf
Sebastian, FL	SEB[3]	Dec 1998	35	15	50	Gulf
Ft. Pierce, FL	FTP	Apr 1996	31	25	56	Atlantic
West Palm Beach, FL	WPB	May 1998	29	25	54	Atlantic
Florida Keys						
Key West, FL	KEY[1]	Mar 1996	41	10	51	Gulf
Key West, FL	KEY[2]	Mar 1997	—	—	29	Gulf
Key West, FL	KEY[3]	Jan 1999	29	19	48	Gulf
Gulf of Mexico (west coast)						
Marco Island, FL	MCI	Apr 1996	29	26	55	Atlantic
Boca Grande, FL	BCG	Apr 1996	31	4	35	Gulf
Sarasota, FL	SAR[1]	Apr 1996	39	5	44	Gulf
Sarasota, FL	SAR[2]	Nov 1996	60	0	60	Gulf
Sarasota, FL	SAR[3]	Apr 1997	55	2	57	Gulf
Sarasota, FL	SAR[4]	Apr 1998	68	2	70	Gulf
Sarasota, FL	SAR[5]	Nov 1998	62	6	68	Gulf
Panama City, FL	PCY	Oct 1996	25	25	50	Gulf

[1] Classification as Atlantic or Gulf migratory group based on the two migratory unit hypothesis where boundaries change seasonally. See text for further details.

to amplification, one of the primers was kinase-labeled with γ^{32}P-ATP by T4 polynucleotide kinase (30 min, 37°C). PCR reactions contained approximately 5 ng of genomic DNA, 0.1 units of *Taq* DNA polymerase, 0.5 μM of each primer, 800 μM dNTPs, 1–2 mM $MgCl_2$, 1X *Taq* buffer at pH 9.0 (Promega, Corp., Madison, WI), and sterile deionized water in a total volume of 10 μL. Thermal cycling was carried out in 96-well plates as follows: denaturation (45 sec, 95°C), annealing (30 sec, temperature as in Appendix Table 1), and polymerization (30 sec, 72°C) for 30 cycles. Aliquots (3 μL) of each PCR reaction were electrophoresed in 6% denaturing polyacrylamide ("sequencing") gels. Gels were dried and exposed to x-ray film. Alleles at individual microsatellites were scored as number of repeats by comparison to the cloned (and sequenced) allele. Genotypes at each microsatellite for each individual were scored and entered into a database.

Initial statistical analysis involved generation of allele frequencies and (direct-count) heterozygosity values, and significance testing of genotypic proportions in relation to those expected under conditions of Hardy-Weinberg equilibrium. Significance testing of Hardy-Weinberg equilibrium proportions involved exact tests performed using Markov-chain randomization (Guo and Thompson, 1992); probability (*P*) values for tests at each microsatellite within each sample were estimated by permutation (bootstrapping) with 1000 resamplings (Manly, 1991). Significance levels for simultaneous tests were adjusted with the sequential Bonferroni approach (Rice, 1989). Tests of genotypic equilibrium at pairs of microsatellites were carried out as a surrogate to assess whether any microsatellites were genetically linked. Probability values for (exact) tests of genotypic equilibrium were generated by 1000 resamplings, and significance levels for simultaneous tests were adjusted with the sequential Bonferroni approach. Allele frequencies and heterozygosity values were obtained by using BIOSYS-1.7 (Swofford and Selander, 1981), and tests of Hardy-Weinberg and genotypic equilibrium employed the package GENEPOP (Raymond and Rousset, 1995). Exact tests also were used to test independence

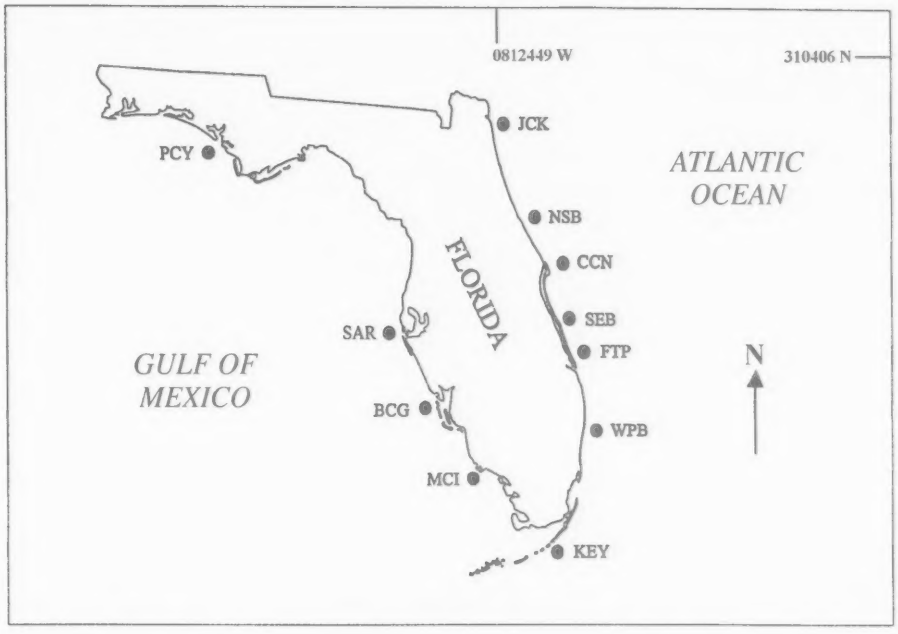

Figure 1

Sampling localities for king mackerel examined in the present study. Acronyms for sample localities are defined in Table 1.

of the distribution of genotypes at each microsatellite with the sex and age of individuals. Initial tests involved each of the 20 samples separately. We then pooled individuals sampled at Atlantic localities (nine samples), in the Florida Keys (three samples), at Gulf localities (eight samples), and over all localities (20 samples) in order to increase cell sizes in individual tests. Probability (P) values for these tests of independence were estimated by permutation (1000 resamplings) and significance levels for simultaneous tests were adjusted with the sequential Bonferroni approach.

Tests of genetic homogeneity among samples included exact tests, as implemented in GENEPOP, the Monte Carlo procedure of Roff and Bentzen (1989), as implemented in the restriction enzyme analysis package of McElroy et al. (1992), and the analysis of molecular variance (AMOVA) of Excoffier et al. (1992). Significance of tests of genetic homogeneity employed permutation with 1000 resamplings per individual comparison, and significance levels for simultaneous tests were adjusted by using the sequential Bonferroni approach. Tests of genetic homogeneity were carried out separately for each of the seven microsatellites. Individual tests were carried out 1) among all 20 samples, 2) among samples (nine) from Atlantic localities, 3) among samples (three) from the Florida Keys, and 4) among samples (eight) from Gulf localities. Analysis of molecular variance (AMOVA) was employed to generate estimates of (genetic) variance components and Φ statistics for the same comparisons. Φ statistics are a set of hierarchical F-statistic analogs that consider evolutionary distance among alleles. Significance of Φ statistics employed permutation (1000 resamplings).

Exact tests, the Monte Carlo procedure of Roff and Bentzen, and AMOVA also were used to assess genetic homogeneity 1) between samples from the Atlantic versus those from the Gulf (excluding samples from the Florida Keys), and 2) among samples from the Atlantic, the Florida Keys, and the Gulf. This design was chosen *a priori*, in part because it was geographically logical, in part because the southern Florida peninsula apparently serves (or has served) as a biogeographic boundary for a number of marine species (Avise, 1992; Gold and Richardson, 1998). The hierarchical capability of AMOVA also permitted a test of homogeneity among samples within the three regional groupings. We also carried out homogeneity testing to examine the temporal stock boundaries currently used in management planning for the king mackerel resource. Each of the 20 samples of king mackerel was designated as either Atlantic or Gulf stock according to the time of year during which they were sampled. Six of the samples thus were designated Atlantic stock and 14 of the samples were designated Gulf stock (Table 1). Genetic homogeneity was then tested between the Atlantic and Gulf "stocks," by using exact tests and the Monte Carlo procedure of Roff and Bentzen.

Clustering of genetic distances, spatial autocorrelation analysis, and assignment tests also were employed to assess temporal and spatial variation of microsatellites.

Table 2

Summary of variation in seven microsatellites among king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys.

Microsatellite	Repeat sequence	No. of alleles	Average heterozygosity ±SE	P_{HW}[1]
Sca-14	$(CA)_6$ TA $(CA)_{13}$	5	0.474 ±0.016	0/20
Sca-23	$(CA)_4$ AAC $(AG)_{12}$	24	0.803 ±0.105	4/20[2]
Sca-37	$(TG)_8$ AG $(TG)_4$ AG $(TG)_4$	9	0.509 ±0.014	0/20
Sca-44	$(CTCG)_2$ CTAT $(CTGT)_5$	8	0.677 ±0.014	0/20
Sca-49	$(TG)_{17}$	15	0.656 ±0.018	0/20
Sca-61	$(CA)_6$ TGTA $(CA)_8$	6	0.311 ±0.018	0/20
Sca-65	$(TG)_{13}$	24	0.798 ±0.016	0/20

[1] Proportion of samples where $P < 0.05$, after Bonferroni correction.

[2] Probability values for three samples (SEB[2], KEY[1], and SAR[4]) were 0.000. The probability value for SAR[1] was 0.006 (adjusted α was 0.003).

Cavalli-Sforza's chord distance (Cavalli-Sforza and Edwards, 1967), as implemented in the GENEDIST program in version 3.4 of the phylogenetic inference package (PHYLIP) of Felsenstein (1992), was used to estimate the degree of genetic divergence or similarity between pairs of samples; neighbor joining (Saitou and Nei, 1987), from the NEIGHBOR program in PHYLIP, was used to cluster the resulting genetic distance matrix. A consensus of 500 neighbor-joining topologies was constructed by using the CONSENSE program in PHYLIP. Spatial autocorrelation analysis was carried out to determine whether allele distributions at each microsatellite at any given sample locality were independent of allele distributions in adjacent localities. Briefly, autocorrelation coefficients (Moran's I values), generated as a function of geographic distance between pairs of sample localities, were used to summarize patterns of geographic variation of allele frequencies at each microsatellite. Positive autocorrelations between adjacent localities, with decreasing autocorrelation as geographic distance between localities increases, are generally interpreted as an isolation-by-distance effect (Sokal and Oden, 1978a). We employed the spatial autocorrelation analysis program (SAAP) of Wartenberg (1989) and followed procedures outlined in Sokal and Oden (1978a, 1978b). "Noise" was minimized by including only alleles that occurred 20 or more times in the data set. The first of two SAAP runs employed equal geographic distances between each of five distance classes; the second employed equal numbers of pairwise comparisons in each distance class. Finally, assignment tests (Paetkau et al., 1995, 1997) were used to "assign" individuals within each of the 20 samples to one of two regional (spatial) groupings, Atlantic or Gulf. The two groupings were employed largely as a result of homogeneity tests of allele distributions, where existence of the two spatial groupings was weakly supported. Assignment tests have a number of uses (Waser and Strobeck, 1998): in this case we were interested in the proportion of individuals within a sample that could be assigned to each regional group, in relation to the locality of the sample and the season in which it was procured. Assignment tests were carried out employing the "assignment calculator" software available at http:\\www.biology.ualberta.ca/jbruzusto/Doh.html.

Results and discussion

Allele frequencies at the seven microsatellites in each of the 20 samples are given in Appendix Tables 2 and 3; number of individuals assayed, heterozygosity (direct count) values, and probability of conformance to expected Hardy-Weinberg proportions per microsatellite per individual sample are given in Appendix Tables 4 and 5. Summary statistics are given in Table 2 and include 1) repeat sequence of the cloned allele, 2) number of alleles detected, 3) average (direct count) heterozygosity (±SE) observed among samples, and 4) results of tests of conformance of observed genotype proportions to expectations of Hardy-Weinberg equilibrium. Cloned alleles at the seven microsatellites included simple (*Sca-49*, *Sca-65*) and complex (*Sca-14*, *Sca-23*, *Sca-37*, *Sca-61*) dinucleotide repeats and one complex tetranucleotide repeat (*Sca-44*). All dinucleotide microsatellites included CA (or complementary TG) repeats, with the number of alleles per microsatellite ranging from five (*Sca-14*) to twenty-four (*Sca-23* and *Sca-65*). Direct count heterozygosity, averaged over the twenty samples, ranged from 0.311 ±0.018 (*Sca-61*) to 0.803 ±0.105 (*Sca-23*). These results indicate that the seven microsatellites assayed in king mackerel are typical of microsatellites found in other vertebrate organisms, including fishes (e.g. DeWoody and Avise, 2000; Turner et al., 1998; Gold et al., 2001).

After sequential Bonferroni correction (Rice, 1989), genotype proportions at six of the microsatellites in all twenty samples did not deviate significantly from proportions expected under Hardy-Weinberg equilibrium. Genotype proportions at *Sca-23* among three of the samples (SEB[2], KEY[1], and SAR[4]) differed significantly (P=0.000) from Hardy-Weinberg equilibrium expectations, and at a fourth sample (SAR[1]), the probability value of 0.006 was very close to the Bonferroni adjusted alpha of 0.003 (Appendix

Table 3

Probability of genotype equilibrium (pairwise comparisons) among seven microsatellite loci in king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys. Corrected α (for initial test) = 0.002.

Microsatellite	*Sca-14*	*Sca-23*	*Sca-37*	*Sca-44*	*Sca-49*	*Sca-61*	*Sca-65*
Sca-14	—	0.389	0.684	0.900	0.665	0.977	0.906
Sca-23		—	0.022	1.000	0.805	0.603	0.194
Sca-37			—	0.724	0.876	0.910	0.430
Sca-44				—	0.328	0.000	0.020
Sca-49					—	0.295	0.998
Sca-61						—	0.873
Sca-65							—

Table 4

Results of tests for spatial homogeneity in allele distribution of seven microsatellites among king mackerel (*Scomberomorus cavalla*) sampled from the east and west coasts of Florida and the Florida Keys. P_{EXACT} = probability based on Fisher's exact tests, with 1000 permutations. P_{RB} = probability based on 1000 bootstrapped replicates (after Roff and Bentzen 1989).

	All samples[1]		Atlantic localities[2]		Florida Keys[3]		Gulf localities[4]	
Test group	P_{EXACT}	P_{RB}	P_{EXACT}	P_{RB}	P_{EXACT}	P_{RB}	P_{EXACT}	P_{RB}
Microsatellite								
Sca-14	0.465	0.447	0.845	0.826	0.510	0.503	0.697	0.668
Sca-23	0.026	0.106	0.250	0.416	0.076	0.068	0.175	0.140
Sca-37	0.431	0.388	0.592	0.498	0.038	0.024	0.592	0.619
Sca-44	0.084	0.073	0.558	0.508	0.111	0.161	0.187	0.136
Sca-49	0.230	0.472	0.487	0.746	0.591	0.529	0.112	0.112
Sca-61	0.278	0.428	0.531	0.563	0.065	0.084	0.273	0.296
Sca-65	0.611	0.588	0.457	0.611	0.910	0.957	0.411	0.169

[1] "All" includes all twenty samples.

[2] Atlantic includes JKV[1]–JKV[2], NSB, CCN, SEB[1]–SEB[3], FTP, and WPB (nine samples total). For explanation of these geographic abbreviations see Table 1.

[3] Keys include KEY[1]–KEY[3] (three samples total).

[4] Gulf includes MCI, BCG, SAR[1]–SAR[5], and PCY (seven samples total).

Tables 4 and 5). F_{IS} values (after Weir and Cockerham, 1984) for these four samples were all positive, indicating a deficit of heterozygotes and the possible presence of a null allele. However, probability values for tests of Hardy-Weinberg equilibrium at *Sca-23* among the remaining 16 samples were nonsignificant and averaged (±SE) 0.385 ±0.076. Although the possibility of a null allele at *Sca-23* cannot be dismissed unequivocally, genotypes at *Sca-23* appear overall to be distributed in accordance with Hardy-Weinberg equilibrium expectation. Finally, tests of genotypic equilibrium between pairs of microsatellites (samples pooled) yielded only one significant value (*Sca-44* × *Sca-61*) following Bonferroni correction (Table 3). Probability values of tests involving these two microsatellites, i.e. *Sca-44* × *Sca-61*, carried out within each of the 20 samples were all nonsignificant and averaged (±SE) 0.338 ±0.067. Of the remaining (pairwise) tests carried out within samples (420 tests in all), only four significant probability values were obtained: *Sca-37* and *Sca-44* (CCN), *Sca-23* × *Sca-44* (PCY), *Sca-37* × *Sca-49* (BCG), and *Sca-23* × *Sca-44* (SEB[2]). These results indicate that genotypes at the seven microsatellites are independent and hence are not linked genetically.

Tests for independence of allele distributions at each of the seven microsatellites versus both sex and age of individuals were carried out 1) within each of the 20 samples, and 2) among individuals (pooled) sampled from the Atlantic, the Florida Keys, the Gulf, and overall. In tests for independence with sex, eight significant probability values ($P<0.05$) were found prior to Bonferroni correction for simultaneous tests (data available from first author). None of these, however, were significant after Bonferroni correc-

Table 5

Results of tests for spatial homogeneity in allele distribution of seven microsatellites between and among pooled samples of king mackerel (*Scomberomorus cavalla*) from the east and west coasts of Florida and the Florida Keys. P_{EXACT} = probability based on Fisher's exact tests, with 1000 permutations. P_{RB} = probability based on 1000 bootstrapped replicates (after Roff and Bentzen 1989). Φ_{CT} = estimate of population subdivision based on AMOVA; P is the probability that Φ_{CT} differs significantly from zero (5000 permutations).

	Comparison of Atlantic[1] with Gulf[2]				Comparison of Atlantic and Keys[3] and Gulf			
	P_{EXACT}	P_{RB}	Φ_{CT}	P	P_{EXACT}	P_{RB}	Φ_{CT}	P
Microsatellite								
Sca-14	0.009	0.006	0.005	0.010	0.020	0.029	0.004	0.031
Sca-23	0.010	0.007	0.001	0.125	0.026	0.081	0.000	0.256
Sca-37	0.426	0.443	−0.001	0.588	0.009	0.001	−0.001	0.794
Sca-44	0.060	0.056	0.004	0.023	0.008	0.004	0.003	0.024
Sca-49	0.506	0.491	−0.001	0.912	0.580	0.535	−0.001	0.707
Sca-61	0.391	0.382	0.001	0.169	0.520	0.689	−0.001	0.398
Sca-65	0.625	0.645	0.004	0.556	0.775	0.508	0.004	0.145

[1] Atlantic includes JKV[1]–JKV[2], NSB, CCN, SEB[1] - SEB[3], FTP, and WPB (nine samples total). For explanation of these geographic abbreviation, see Table 1.

[2] Gulf includes MCI, BCG, SAR[1]–SAR[5], and PCY (seven samples total).

[3] Keys includes KEY[1]–KEY[3] (three samples total).

tion. In addition, one would expect that eight of 162 tests would be significant by chance alone at $\alpha = 0.05$. Finally, only one of the significant probability values occurred in a pooled comparison (*Sca-49* in the test of individuals from the Atlantic), where larger sample sizes were expected to increase robustness of tests of independence. In tests for independence of allele distributions with the age (year class) of individuals, eight significant probability values ($P<0.05$) were found prior to Bonferroni correction for simultaneous tests (data available from first author), two of which (*Sca-23* in SAR[4] and *Sca-61* in SAR[4]) were significant after Bonferroni correction with the use of eight simultaneous tests per microsatellite to estimate adjusted α levels. In both instances, nonindependence appeared to stem from an elevated incidence of specific alleles: *Sca-23*19* occurred at a frequency of 36% in the 1989 year class, as opposed to other year classes where its frequency ranged from 0% to 15%; and similarly, *Sca61*12* occurred at a frequency of 25–30% in the 1986 and 1989 year classes, as opposed to a frequency of 0–10% in the other year classes. We suspect these are anomalous instances that do not reflect an age-related effect, in part because allele distributions at *Sca-23* and *Sca-61* were independent of year class in all other samples, and in part because allele distributions at all microsatellites were independent of year class in pooled comparisons, where larger sample sizes should increase robustness of tests of independence. We concluded that allelic variation at the seven microsatellites essentially is independent of variation in both sex and age (year class).

Spatial homogeneity in allele distributions at each microsatellite was tested 1) over all 20 samples, 2) among samples from the Atlantic, 3) among samples from the Florida Keys, and 4) among samples from the Gulf. Only three significant probability values were found prior to Bonferroni correction: the exact test at *Sca-23* in the comparison over all 20 samples, and both the exact test and the Roff-Bentzen procedure at *Sca-37* in the comparison among samples from the Florida Keys (Table 4). None of the probability values were significant after Bonferroni correction. Tests for spatial homogeneity 1) between pooled samples from the Atlantic versus pooled samples from the Gulf, and 2) among pooled samples from the Atlantic, Florida Keys, and Gulf, indicated that all three regional groupings differed genetically from one another (Table 5). For the comparison Atlantic versus Gulf, significant heterogeneity prior to Bonferroni correction was found at *Sca-14* (all three statistical approaches), *Sca-23* (exact test and the Roff-Bentzen procedure), and *Sca-44* (for the probability that $\Phi_{CT}>0$). Probability values for *Sca-14* and *Sca-23* were marginal in relation to the (initial) Bonferroni adjusted α of 0.007, whereas the probability that Φ_{CT} > zero at *Sca-44* was nonsignificant after Bonferroni correction (Table 5). For the comparison of Atlantic, Florida Keys, and Gulf samples, significant heterogeneity was found at *Sca-14* (all three statistical approaches) and *Sca23* (exact test only) before but not after Bonferroni correction; heterogeneity at *Sca-37* and *Sca-44* in the same comparison was significant both before and after Bonferroni correction in at least one of the three statistical approaches (Table 5). Frequency differences at *Sca-14*, *Sca-23*, and *Sca-44* among the three regional groupings are shown in Table 6 and indicate that small differences in frequency of several alleles at each microsatellite appear to account for observed heterogeneity among the pooled sample comparisons.

Table 6

Allele frequencies at *Sca 14* and *Sca 23* for king mackerel (*Scomberomorus cavalla*) from the Atlantic, Florida Keys, and Gulf. Allele numbers represent the size in base pairs of the fragment amplified.

Microsatellite (allele)	Atlantic	Florida Keys	Gulf
Sca-14			
91	0.017	0.004	0.006
93	0.053	0.058	0.034
95	0.670	0.667	0.735
97	0.233	0.240	0.200
99	0.029	0.031	0.027
Sca-23			
138	0.063	0.054	0.052
140	0.028	0.050	0.028
142	0.221	0.250	0.241
144	0.012	0.008	0.005
146	0.131	0.092	0.121
148	0.026	0.008	0.015
150	0.146	0.108	0.132
152	0.185	0.177	0.149
154	0.008	0.011	0.015
156	0.100	0.111	0.109
158	0.011	0.011	0.011
160	0.009	0.011	0.012
162	0.001	0.000	0.001
164	0.015	0.027	0.016
166	0.002	0.004	0.009
168	0.002	0.004	0.000
170	0.009	0.019	0.018
172	0.017	0.019	0.039
174	0.009	0.015	0.010
176	0.002	0.008	0.009
178	0.002	0.008	0.001
180	0.001	0.004	0.002
182	0.000	0.000	0.002
184	0.002	0.000	0.000
Sca44			
153	0.004	0.015	0.009
157	0.084	0.046	0.090
161	0.030	0.019	0.041
165	0.366	0.308	0.295
169	0.398	0.465	0.438
173	0.104	0.131	0.118
177	0.012	0.011	0.010
181	0.000	0.004	0.000

In general, results of the three approaches to homogeneity testing were fairly consistent, with one notable exception. At *Sca-37*, probability values from the exact test and the Roff-Bentzen procedure were 0.009 and 0.001 in the comparison of Atlantic, Florida Keys, and Gulf samples, respectively, whereas the probability that Φ_{CT} differed from zero was 0.794 (Table 5). We examined this discrepancy further by carrying out "V" tests of homogeneity (DeSalle et al. 1987) for each allele at *Sca-37*. Significant heterogeneity ($P<0.05$) was found only at *Sca-37*12*: this allele was found only in the March 1997 sample from the Florida Keys (KEY^2), where it occurred at a frequency of 6.9% (Appendix Tables 2 and 3). Because there were far fewer alleles at *Sca-37* sampled from the Florida Keys (258) than from either the Atlantic (884) or Gulf (872), the disproportionate frequency of this allele within the Florida Keys likely accounts for the significance encountered in the exact test and the Roff-Bentzen procedure. Given the absence of this allele in two of the three samples from the Florida Keys, we do not believe the significant heterogeneity detected at *Sca-37* is meaningful biologically.

Although homogeneity testing of pooled samples indicated that samples from the Atlantic differed from samples from the Gulf at *Sca-14* and *Sca-23*, and that samples from the Florida Keys differed from the other two at *Sca-44*, the allele-frequency differences were small and accounted for only a fraction of the overall genetic variance. Results of AMOVA for the comparison of Atlantic with Gulf samples revealed that on average 99.74% of the total genetic variance at the seven microsatellites occurred within samples, as compared to only 0.19% between regions. For the comparison of Atlantic, Florida Keys, and Gulf samples, 99.78% of the genetic variance on average occurred within samples, whereas only 0.11% occurred among regions. For both comparisons, the proportion of the variation among samples within regions accounted for the remainder of the genetic variance, and for both comparisons, this proportion was small and statistically nonsignificant.

Finally, homogeneity tests were used to examine the temporal stock boundaries currently used in management of the king mackerel resource by classifying each of the 20 samples as either Atlantic or Gulf stock (Table 1). No significant heterogeneity at any of the seven microsatellites was found, providing no genetic evidence for existence of temporal boundaries dividing Atlantic and Gulf migratory units (stocks).

Neighbor joining of Cavalli-Sforza's chord distances between pairs of samples yielded little evidence of geographic structure among the 20 samples. With few exceptions, samples from the same or geographically proximate localities did not cluster together, and most nodes in the topology (available from the first author) were supported by well less than 50% of bootstrap proportions. Spatial autocorrelation (SAAP) analysis also indicated the absence of a relationship between allele frequency and geographic distance. Initially, SAAP analysis employed both equal geographic distances between each of five distance classes and equal numbers of pairwise comparisons in each distance class. Analysis involving equal geographic distances between distance classes generated an uneven number of pairwise comparisons among distance classes, i.e. 18, 14, 15, 5, and 3 pairwise comparisons in distance classes 1–5, respectively, resulting in a high variance in Moran's I values among alleles in distance classes 4 and 5. Accordingly, the analysis was restricted to equal numbers of pairwise

comparisons (eleven) in each distance class. A total of 50 alleles (five at *Sca-14*, sixteen at *Sca-23*, four at *Sca-37*, six at *Sca-44*, five at *Sca-49*, three at *Sca-61*, and eleven at *Sca-65*) was tested, resulting in 250 Moran's I values. Only 10 significant ($P<0.05$) Moran's I values were generated: one at *Sca-14* (positive in the third distance class); seven at *Sca-23* (two positive in the second distance class, four positive in the third distance class, and one negative in the fifth distance class); two at *Sca-37* (one negative in the fourth distance class and one positive in the fifth distance class), and one at *Sca-65* (negative in the fifth distance class). No significant Moran's I values were found at *Sca-44*, *Sca-49*, and *Sca-61*. Only one of the "significant" Moran's I values (a positive value for *Sca-23*22* in the third distance class) remained significant after Bonferroni correction. The general absence of spatial autocorrelation indicates that gene flow in king mackerel is consistent with expectations of an island model (*sensu* Wright, 1943) of population structure, meaning that there is roughly an equal probability of gene flow between any of the 20 sample localities.

Assignment tests generally were concordant with other analyses of king mackerel microsatellites in that fish from the Atlantic appeared to be weakly divergent genetically from fish in the Gulf. Each of the 20 samples included high proportions of both Atlantic and Gulf fish, and there appeared to be no strong geographic pattern in proportion of fish assigned to either Atlantic or Gulf groups (Table 7). On average, samples from the Atlantic contained more "Atlantic" fish (54%), whereas samples from the Gulf contained more "Gulf" fish (51.2%). The three samples from the Florida Keys, on average, contained more "Atlantic" fish (53.3%), but this finding is misleading because the proportion of "Atlantic" fish in the three samples from the Florida Keys ranged from 37.2% to 64.0% (Table 7). In addition, the estimated proportions of Atlantic versus Gulf fish in samples from the Florida Keys were not consistent with what might be predicted based on the time of sampling and the spatial-temporal boundaries used currently in king mackerel stock assessment. The KEY[1] and KEY[2] samples were obtained in March, a time when both would be considered Gulf stock, yet close to the temporal boundary (1 April) when they would be considered Atlantic stock. The estimated proportion of Gulf fish in these two samples was 62.8% (KEY[1]) and 41.4% (KEY[2]). Alternatively, the KEY[3] sample was obtained in January when king mackerel in the Florida Keys are considered Gulf stock. The estimated proportion of Gulf fish in the KEY[3] sample was 36.0%.

Table 7

Assignment (as percentage) of individuals from 20 samples of king mackerel (*Scomberomorus cavalla*) from the east and west coast of Florida and the Florida Keys to either "Atlantic" or "Gulf" group.

	Assigned group	
Sample	Atlantic	Gulf
Atlantic Ocean		
JCK[1]	51.8	48.2
JCK[2]	62.5	37.5
NSB	58.0	42.0
CCN	46.0	54.0
SEB[1]	58.0	42.0
SEB[2]	62.0	38.0
SEB[3]	52.0	48.0
FTP	53.6	46.4
WPB	41.8	58.2
Avg.	54.0	46.0
Florida Keys		
KEY[1]	37.2	62.8
KEY[2]	58.6	41.4
KEY[3]	64.0	36.0
Avg.	53.3	46.7
Gulf of Mexico		
MCI	49.1	50.9
BCG	45.7	54.3
SAR[1]	46.8	53.2
SAR[2]	53.3	46.7
SAR[3]	53.6	46.4
SAR[4]	41.1	58.6
SAR[5]	54.3	45.7
PCY	46.0	54.0
Avg.	48.8	51.2

Synopsis and conclusions

Genetic data obtained in our study are compatible with the hypothesis that two, weakly differentiated "genetic" subpopulations of king mackerel exist in waters off Florida and that considerable, perhaps extensive, mixing occurs between them. King mackerel sampled from the Florida Keys cannot be assigned unequivocally to either "genetic" stock; all collections tested appeared to be mixtures, with approximately equal proportions of fish from the two "genetic" stocks. These results are not consistent with the current spatial-temporal boundaries employed in stock assessment and allocation of the king mackerel resource. Results are consistent with the hypothesis that considerable gene flow occurs among all of the localities sampled, and that differences in gene flow likely do not arise as a function of geographic distance. Similar findings were obtained by Gold et al. (1997) in their study of variation in king mackerel mitochondrial DNA. The genetic differences between king mackerel in the Atlantic versus those in the Gulf most likely stem from reduced gene flow (migration) between the Atlantic and Gulf in relation to gene flow (migration) along the Atlantic and Gulf coasts of peninsular Florida. This is consistent with the notion based on studies of other marine fishes (Avise et al., 1992; Gold and Richardson, 1998) that the southern Florida peninsula serves (or has served) as a biogeographic boundary.

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Appendix Table 1

Microsatellites employed for king mackerel (*Scomberomorus cavalla*).

Microsatellite	Primer sequence (5′ → 3′) (forward and reverse, respectively)	Length (base pairs)	Annealing temperature (°C)
Sca-14	ATT CCC CAA ACA ATA CAC AC AGT GGA CGA CCC ATT CTA C	93	56
Sca-23	AGC CCT CTT ACA ATC TGC TAC CC AAA CCT TTA AGG CCT CAA GTA AAG	146	58
Sca-37	GCG CCG TGA CTT TTT ATT GCT C CAA CAA TTA GTC GCA GCC CTA G	154	58
Sca-44	ATG GCC AAA TGG CAC ATA ATC A GGG CAG CTC CAT GGG TCT GAG T	169	58
Sca-49	AGA TGT GAC AAC AGT GGG ATG GCA GCA GTA ATA AAG	157	56
Sca-61	GGT ACT GTC GGG AGA ATG AGA T TGA ATT TTA TAT GGA GGG TCT G	228	56
Sca-65	AGC TGC TGC CAT GAT TTG TT TCC TCC ACT GCC CCT TTC TT	129	52

Appendix Table 2

Allele frequencies at microsatellites in king mackerel (*Scomberomorus cavalla*). Legend to samples: JKV[1] = Jacksonville, Florida (July 1996); JKV[2] = Jacksonville, Florida (July, 1998); NSB = New Smryna Beach, Florida (July 1996); CCN = Cape Canaveral, Florida (December 1998); SEB[1] = Sebastian, Florida (March 1997); SEB[2] = Sebastian, Florida (March 1998); SEB[3] = Sebastian, Florida (December 1998); FTP = Ft. Pierce, Florida (April 1996); WPB = West Palm Beach, Florida (May 1998); KEY[1] = Key West, Florida (March 1996).

	Sample									
Microsatellite (allele)[1]	JKV[1]	JKV[2]	NSB	CCN	SEB[1]	SEB[2]	SEB[3]	FTP	WPB	KEY[1]
Sca-14										
91	0.000	0.031	0.040	0.030	0.010	0.030	0.000	0.009	0.009	0.010
93	0.046	0.063	0.070	0.040	0.041	0.070	0.050	0.063	0.037	0.030
95	0.741	0.719	0.650	0.630	0.735	0.590	0.670	0.643	0.667	0.680
97	0.185	0.188	0.220	0.250	0.184	0.280	0.250	0.259	0.259	0.260
99	0.028	0.000	0.020	0.050	0.031	0.030	0.030	0.027	0.028	0.020
Sca-23										
138	0.046	0.016	0.060	0.080	0.090	0.030	0.060	0.091	0.073	0.029
140	0.019	0.032	0.030	0.050	0.020	0.000	0.060	0.027	0.018	0.039
142	0.231	0.210	0.120	0.250	0.230	0.230	0.210	0.236	0.264	0.265
144	0.009	0.016	0.000	0.020	0.020	0.000	0.010	0.018	0.018	0.000
146	0.102	0.129	0.140	0.100	0.140	0.170	0.140	0.127	0.136	0.147
148	0.019	0.048	0.030	0.000	0.060	0.010	0.010	0.036	0.027	0.020
150	0.176	0.161	0.140	0.180	0.120	0.190	0.100	0.155	0.100	0.088
152	0.241	0.177	0.180	0.120	0.180	0.280	0.150	0.145	0.191	0.098
154	0.009	0.016	0.000	0.010	0.010	0.000	0.000	0.018	0.009	0.020
156	0.111	0.113	0.130	0.110	0.060	0.050	0.140	0.064	0.091	0.118
158	0.019	0.016	0.020	0.020	0.000	0.000	0.010	0.000	0.018	0.020
160	0.000	0.016	0.020	0.000	0.010	0.010	0.030	0.000	0.000	0.000
162	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
164	0.009	0.016	0.030	0.010	0.000	0.030	0.020	0.009	0.009	0.039
166	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.009	0.000
168	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.009	0.000	0.010
170	0.009	0.016	0.010	0.020	0.000	0.000	0.010	0.018	0.000	0.039
172	0.000	0.016	0.060	0.010	0.030	0.000	0.010	0.018	0.009	0.029
174	0.000	0.000	0.020	0.000	0.010	0.000	0.010	0.018	0.018	0.010
176	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.010
178	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.010
180	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.010
182	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
184	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000
Sca-37										
138	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
142	0.000	0.031	0.030	0.000	0.000	0.010	0.010	0.000	0.000	0.020
144	0.667	0.688	0.600	0.694	0.720	0.630	0.540	0.623	0.630	0.637
146	0.009	0.016	0.040	0.010	0.030	0.010	0.030	0.019	0.019	0.000
148	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
150	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
152	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
154	0.296	0.266	0.320	0.286	0.240	0.330	0.400	0.330	0.286	0.333
156	0.019	0.000	0.000	0.010	0.010	0.020	0.020	0.028	0.010	0.010
Sca44										
153	0.000	0.000	0.000	0.010	0.000	0.000	0.010	0.018	0.000	0.020
157	0.066	0.078	0.110	0.120	0.060	0.080	0.090	0.098	0.056	0.069
161	0.038	0.047	0.030	0.020	0.030	0.040	0.010	0.027	0.037	0.020
165	0.387	0.469	0.390	0.300	0.390	0.310	0.290	0.420	0.370	0.275
169	0.396	0.281	0.380	0.420	0.410	0.470	0.500	0.357	0.333	0.471
173	0.104	0.109	0.090	0.110	0.100	0.090	0.070	0.071	0.194	0.147
177	0.009	0.016	0.000	0.020	0.010	0.010	0.030	0.009	0.009	0.000
181	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

continued

Appendix Table 2 (continued)

Microsatellite (allele)[1]	Sample									
	JKV[1]	JKV[2]	NSB	CCN	SEB[1]	SEB[2]	SEB[3]	FTP	WPB	KEY[1]
Sca-49										
139	0.009	0.000	0.000	0.000	0.000	0.000	0.010	0.009	0.000	0.000
141	0.046	0.109	0.060	0.000	0.043	0.020	0.020	0.036	0.037	0.067
143	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
145	0.546	0.547	0.490	0.590	0.435	0.690	0.580	0.518	0.481	0.533
147	0.167	0.203	0.150	0.130	0.207	0.100	0.170	0.188	0.167	0.178
149	0.019	0.031	0.060	0.030	0.033	0.030	0.030	0.018	0.046	0.000
151	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
153	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
155	0.009	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
157	0.046	0.031	0.090	0.070	0.076	0.060	0.080	0.063	0.093	0.089
159	0.130	0.063	0.130	0.170	0.196	0.090	0.090	0.161	0.148	0.111
161	0.009	0.016	0.000	0.010	0.011	0.010	0.010	0.009	0.009	0.011
163	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.009	0.000
165	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
167	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000
Sca 61										
208	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
210	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
224	0.083	0.078	0.100	0.041	0.071	0.102	0.130	0.074	0.046	0.088
226	0.139	0.063	0.050	0.112	0.061	0.071	0.090	0.065	0.083	0.137
228	0.769	0.859	0.850	0.847	0.857	0.827	0.780	0.861	0.861	0.765
230	0.009	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.009	0.000
Sca 65										
117	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
123	0.380	0.422	0.360	0.430	0.440	0.350	0.360	0.384	0.464	0.438
125	0.028	0.047	0.040	0.050	0.030	0.080	0.040	0.063	0.036	0.063
127	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.010
129	0.065	0.016	0.130	0.060	0.080	0.090	0.130	0.036	0.036	0.073
131	0.037	0.094	0.030	0.030	0.020	0.000	0.030	0.018	0.000	0.042
133	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.009	0.009	0.000
135	0.241	0.219	0.200	0.170	0.150	0.280	0.200	0.223	0.209	0.219
137	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
139	0.000	0.000	0.000	0.010	0.010	0.010	0.000	0.018	0.018	0.000
141	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000
143	0.009	0.000	0.000	0.010	0.020	0.010	0.000	0.009	0.018	0.010
147	0.093	0.047	0.150	0.080	0.080	0.070	0.150	0.080	0.109	0.063
149	0.028	0.016	0.010	0.020	0.020	0.010	0.010	0.018	0.009	0.021
151	0.009	0.016	0.020	0.040	0.030	0.030	0.020	0.045	0.018	0.000
153	0.046	0.016	0.020	0.000	0.040	0.020	0.020	0.045	0.027	0.031
155	0.037	0.031	0.020	0.050	0.010	0.020	0.020	0.036	0.027	0.010
157	0.019	0.016	0.010	0.030	0.020	0.020	0.010	0.009	0.000	0.000
159	0.000	0.016	0.000	0.020	0.010	0.000	0.000	0.000	0.000	0.000
161	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
163	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
165	0.000	0.016	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
167	0.009	0.031	0.010	0.000	0.010	0.000	0.010	0.000	0.000	0.000
171	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

[1] Allele number represents size in base pairs of the fragment amplified.

Appendix Table 3

Allele frequencies at microsatellites in king mackerel (*Scomberomorus cavalla*). Legend to samples: KEY[2] = Key West, Florida (March 1997); KEY[3] = Key West, Florida (January 1999); MCI = Marco Island, Florida (April 1996); BCG = Boca Grande, Florida (April 1996); SAR[1] = Treasure Island, Florida (April 1996); SAR[2] = Treasure Island, Florida (November 1996); SAR[3] = Treasure Island, Florida (April 1997); SAR[4] = Treasure Island, Florida (April 1998); SAR[5] = Treasure Island, Florida (November 1998); PCY = Panama City, Florida (October 1996).

	Sample									
Microsatellite (allele)[1]	KEY[2]	KEY[3]	MCI	BCG	SAR[1]	SAR[2]	SAR[3]	SAR[4]	SAR[5]	PCY
Sca-14										
91	0.000	0.000	0.009	0.014	0.000	0.009	0.009	0.000	0.007	0.000
93	0.069	0.080	0.036	0.057	0.033	0.018	0.063	0.021	0.036	0.020
95	0.724	0.620	0.745	0.771	0.685	0.764	0.741	0.771	0.714	0.680
97	0.190	0.250	0.173	0.143	0.250	0.200	0.170	0.186	0.221	0.230
99	0.017	0.050	0.036	0.014	0.033	0.009	0.018	0.021	0.021	0.070
Sca 23										
138	0.086	0.060	0.018	0.057	0.096	0.033	0.027	0.036	0.096	0.060
140	0.017	0.080	0.027	0.029	0.032	0.017	0.027	0.043	0.029	0.020
142	0.224	0.250	0.309	0.257	0.266	0.217	0.200	0.239	0.250	0.200
144	0.017	0.010	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.020
146	0.069	0.050	0.145	0.171	0.064	0.183	0.118	0.109	0.103	0.080
148	0.000	0.000	0.018	0.000	0.032	0.008	0.009	0.029	0.007	0.010
150	0.121	0.120	0.155	0.043	0.160	0.108	0.173	0.130	0.132	0.130
152	0.207	0.240	0.136	0.157	0.117	0.142	0.164	0.174	0.176	0.110
154	0.000	0.010	0.000	0.029	0.011	0.017	0.009	0.007	0.022	0.030
156	0.086	0.120	0.045	0.157	0.117	0.117	0.127	0.109	0.096	0.130
158	0.017	0.000	0.000	0.000	0.021	0.008	0.027	0.007	0.000	0.030
160	0.052	0.000	0.027	0.014	0.000	0.033	0.000	0.014	0.000	0.010
162	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000
164	0.034	0.010	0.000	0.029	0.000	0.033	0.018	0.014	0.022	0.010
166	0.017	0.000	0.009	0.014	0.000	0.000	0.009	0.007	0.000	0.040
168	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
170	0.000	0.010	0.027	0.014	0.011	0.025	0.009	0.014	0.015	0.030
172	0.017	0.010	0.036	0.014	0.064	0.025	0.036	0.036	0.037	0.060
174	0.017	0.020	0.018	0.000	0.000	0.017	0.009	0.007	0.015	0.010
176	0.000	0.010	0.027	0.014	0.000	0.000	0.009	0.007	0.000	0.020
178	0.017	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
180	0.000	0.000	0.000	0.000	0.000	0.017	0.000	0.000	0.000	0.000
182	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.007	0.000	0.000
184	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sca-37										
138	0.069	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
142	0.034	0.000	0.009	0.000	0.000	0.017	0.009	0.007	0.000	0.023
144	0.603	0.653	0.627	0.700	0.628	0.642	0.679	0.600	0.579	0.593
146	0.000	0.010	0.018	0.043	0.021	0.025	0.036	0.007	0.007	0.000
148	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000
150	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
152	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
154	0.276	0.327	0.327	0.257	0.319	0.292	0.250	0.343	0.379	0.349
156	0.017	0.010	0.018	0.000	0.032	0.017	0.027	0.043	0.036	0.035
Sca-44										
153	0.034	0.000	0.009	0.014	0.000	0.017	0.000	0.029	0.000	0.000
157	0.069	0.010	0.056	0.100	0.096	0.133	0.089	0.114	0.072	0.050
161	0.052	0.000	0.037	0.014	0.032	0.008	0.098	0.036	0.051	0.040
165	0.276	0.360	0.259	0.314	0.255	0.300	0.268	0.293	0.355	0.300
169	0.431	0.480	0.546	0.443	0.436	0.408	0.455	0.393	0.413	0.430
173	0.121	0.120	0.093	0.100	0.170	0.133	0.080	0.129	0.087	0.160
177	0.017	0.020	0.000	0.014	0.011	0.000	0.009	0.007	0.022	0.020
181	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

continued

Appendix Table 3 (continued)

Microsatellite (allele)[1]	Sample									
	KEY[2]	KEY[3]	MCI	BCG	SAR[1]	SAR[2]	SAR[3]	SAR[4]	SAR[5]	PCY
Sca-49										
139	0.000	0.000	0.009	0.000	0.011	0.010	0.009	0.000	0.000	0.000
141	0.069	0.070	0.055	0.043	0.054	0.031	0.054	0.043	0.036	0.020
143	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.007	0.000	0.000
145	0.621	0.580	0.464	0.457	0.576	0.594	0.455	0.614	0.529	0.560
147	0.121	0.100	0.218	0.200	0.076	0.156	0.152	0.114	0.200	0.180
149	0.017	0.040	0.009	0.029	0.011	0.010	0.027	0.014	0.014	0.060
151	0.000	0.000	0.009	0.014	0.000	0.000	0.000	0.007	0.000	0.000
153	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
155	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
157	0.052	0.080	0.100	0.129	0.076	0.063	0.089	0.021	0.071	0.050
159	0.086	0.130	0.118	0.129	0.141	0.135	0.196	0.171	0.143	0.130
161	0.034	0.000	0.018	0.000	0.000	0.000	0.009	0.007	0.000	0.000
163	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
165	0.000	0.000	0.000	0.000	0.022	0.000	0.009	0.000	0.000	0.000
167	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000
Sca-61										
208	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000
210	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
224	0.052	0.130	0.073	0.086	0.054	0.138	0.127	0.107	0.100	0.070
226	0.017	0.100	0.055	0.143	0.098	0.078	0.100	0.114	0.121	0.070
228	0.931	0.760	0.873	0.757	0.837	0.776	0.755	0.779	0.771	0.860
230	0.999	0.010	0.000	0.014	0.000	0.000	0.018	0.000	0.007	0.000
Sca-65										
117	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010
123	0.483	0.460	0.364	0.357	0.436	0.446	0.375	0.357	0.386	0.340
125	0.017	0.030	0.036	0.100	0.064	0.045	0.071	0.086	0.043	0.060
127	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
129	0.052	0.080	0.055	0.057	0.032	0.054	0.063	0.057	0.021	0.060
131	0.000	0.020	0.027	0.000	0.064	0.036	0.018	0.071	0.029	0.020
133	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
135	0.207	0.160	0.273	0.300	0.245	0.179	0.205	0.193	0.243	0.190
137	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.010
139	0.000	0.010	0.000	0.000	0.000	0.009	0.009	0.007	0.007	0.000
141	0.000	0.000	0.018	0.000	0.000	0.000	0.000	0.000	0.000	0.010
143	0.017	0.010	0.000	0.014	0.000	0.036	0.009	0.000	0.007	0.000
147	0.103	0.110	0.073	0.029	0.053	0.080	0.080	0.100	0.114	0.090
149	0.034	0.020	0.036	0.057	0.021	0.000	0.018	0.014	0.029	0.020
151	0.017	0.040	0.055	0.000	0.000	0.009	0.018	0.014	0.021	0.040
153	0.034	0.030	0.018	0.029	0.021	0.036	0.054	0.029	0.029	0.090
155	0.017	0.020	0.018	0.014	0.032	0.027	0.045	0.021	0.029	0.050
157	0.017	0.010	0.018	0.014	0.011	0.018	0.027	0.014	0.029	0.010
159	0.000	0.000	0.000	0.014	0.000	0.000	0.009	0.014	0.000	0.000
161	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.007	0.000	0.000
163	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
165	0.000	0.000	0.000	0.000	0.000	0.018	0.000	0.000	0.000	0.000
167	0.000	0.000	0.000	0.014	0.021	0.000	0.000	0.014	0.007	0.000
171	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000

[1] Allele number represents size in base pairs of the fragment amplified.

Appendix Table 4

Summary statistics for each of seven microsatellites among samples of king mackerel (*Scomberomorus cavalla*): n = number of individuals assayed; H_{DC} = direct-count heterozygosity; and P_{HW} = probability that genotypes conform to expectations of Hardy-Weinberg equilibrium. Legends to sample localities are given in Appendix Table 2.

Microsatellite	JKV[1]	JKV[2]	NSB	CCN	SEB[1]	SEB[2]	SEB[3]	FTP	WPB	KEY[1]
Sca-14										
n	54	32	50	50	49	50	50	56	54	50
H_{DC}	0.481	0.375	0.460	0.500	0.408	0.600	0.420	0.571	0.537	0.520
P_{HW}	0.710	0.297	0.141	0.354	0.333	0.431	0.440	0.203	0.070	0.103
Sca-23										
n	54	31	50	50	50	50	50	55	55	51
H_{DC}	0.833	0.806	0.780	0.840	0.820	0.600	0.800	0.855	0.800	0.765
P_{HW}	0.571	0.094	0.121	0.618	0.654	0.000	0.141	0.085	0.483	0.000
Sca-37										
n	54	32	50	49	50	50	50	53	54	51
H_{DC}	0.500	0.531	0.540	0.449	0.380	0.520	0.560	0.585	0.463	0.608
P_{HW}	0.039	0.306	0.903	0.193	0.607	1.000	0.784	0.291	0.293	0.069
Sca-44										
n	53	32	50	50	50	50	50	56	54	51
H_{DC}	0.604	0.719	0.720	0.680	0.720	0.620	0.660	0.643	0.722	0.569
P_{HW}	0.584	0.965	0.911	0.518	0.583	0.618	0.719	0.875	0.095	0.095
Sca-49										
n	54	32	50	49	46	50	50	56	54	45
H_{DC}	0.611	0.656	0.820	0.680	0.739	0.540	0.620	0.696	0.704	0.600
P_{HW}	0.722	0.543	0.871	0.509	0.290	0.753	0.313	0.958	0.943	0.571
Sca-61										
n	54	32	50	49	49	49	50	54	54	51
H_{DC}	0.407	0.281	0.280	0.306	0.224	0.306	0.360	0.204	0.278	0.392
P_{HW}	1.000	1.000	0.709	1.000	0.152	0.306	0.703	0.093	1.000	0.851
Sca-65										
n	54	32	50	50	50	50	50	56	55	48
H_{DC}	0.870	0.813	0.900	0.900	0.820	0.800	0.780	0.839	0.727	0.729
P_{HW}	0.975	0.388	0.647	0.985	0.777	0.242	0.917	0.978	0.479	0.838

Appendix Table 5

Summary statistics for each of seven microsatellites among samples of king mackerel (*Scomberomorus cavalla*): n = number of individuals assayed; H_{DC} = direct-count heterozygosity; and P_{HW} = probability that genotypes conform to expectations of Hardy-Weinberg equilibrium. Legends to sample localities are in Appendix Table 2.

Microsatellite (allele)	KEY[2]	KEY[3]	MCI	BCG	SAR[1]	SAR[2]	SAR[3]	SAR[4]	SAR[5]	PCY
Sca-14										
n	29	50	55	35	46	55	56	70	70	50
H_{DC}	0.517	0.500	0.473	0.371	0.543	0.345	0.429	0.414	0.500	0.520
P_{HW}	0.760	0.143	0.246	0.042	0.562	0.403	0.690	0.540	0.824	0.336
Sca-23										
n	29	50	55	35	47	60	55	69	68	50
H_{DC}	0.897	0.760	0.745	0.886	0.723	0.800	0.855	0.783	0.838	0.880
P_{HW}	0.416	0.106	0.032	0.947	0.006	0.039	0.846	0.000	0.647	0.365
Sca-37										
n	29	50	55	35	47	60	55	69	68	50
H_{DC}	0.552	0.469	0.491	0.486	0.447	0.617	0.446	0.571	0.543	0.419
P_{HW}	0.092	0.647	0.384	0.851	0.079	0.431	0.817	0.499	0.785	0.235
Sca-44										
n	29	50	54	35	47	60	56	70	70	50
H_{DC}	0.828	0.560	0.611	0.686	0.723	0.633	0.696	0.714	0.739	0.700
P_{HW}	0.686	0.219	0.953	0.722	0.353	0.495	0.335	0.813	0.132	0.050
Sca-49										
n	29	50	55	35	46	48	56	70	70	50
H_{DC}	0.586	0.580	0.727	0.771	0.630	0.625	0.714	0.500	0.686	0.640
P_{HW}	0.667	0.055	0.679	0.153	0.098	0.806	0.303	0.246	0.847	0.856
Sca-61										
n	29	50	55	35	46	58	55	70	70	50
H_{DC}	0.138	0.480	0.218	0.343	0.326	0.379	0.327	0.314	0.371	0.280
P_{HW}	1.000	0.486	0.390	0.073	1.000	0.348	0.016	0.105	0.364	1.000
Sca-65										
n	29	50	55	35	47	56	56	70	70	50
H_{DC}	0.690	0.800	0.727	0.743	0.681	0.696	0.839	0.843	0.886	0.880
P_{HW}	0.581	0.656	0.317	0.615	0.250	0.425	0.526	0.879	0.183	0.942

Abstract—Catch rates in the South African rock lobster (*Jasus lalandii*) fishery declined after 1989 in response to reduced adult somatic growth rates and a consequent reduction in recruitment to the fishable population. Although spatial and temporal trends in adult growth are well described, little is known about how juvenile growth rates have been affected. In our study, growth rates of juvenile rock lobster on Cape Town harbor wall were compared with those recorded at the same site more than 25 years prior to our study, and with those on a nearby natural nursery reef. We found that indices of somatic growth measured during 1996–97 at the harbor wall had declined significantly since 1971–72. Furthermore, growth was slower among juvenile *J. lalandii* at the harbor wall than those at the natural nursery reef. These results suggest that growth rates of juvenile and adult *J. lalandii* exhibit similar types of spatiotemporal patterns. Thus, the recent coastwide decline in adult somatic growth rates might also encompass smaller size classes.

Do fluctuations in the somatic growth rate of rock lobster (*Jasus lalandii*) encompass all size classes? A re-assessment of juvenile growth

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The South African fishery for rock lobster (*Jasus lalandii*) began in the late nineteenth century and expanded rapidly so that catches peaked at approximately 10,000 metric tons (t) per annum between 1950 and 1965 (Pollock, 1986). However, subsequent deterioration in catches in the 1960s and 1970s was arrested only in the mid-1980s by the implementation of a management approach centered on an annual total allowable catch (TAC). Over the following five years, catches were maintained at apparently sustainable levels of 3500–4000 t per annum (Cockcroft and Payne, 1999), still representing the largest yield of any *Jasus* species at that time (Pollock, 1986). However, the period of stability ended after 1989, when catch rates declined in response to reduced adult somatic growth rates and a concomitant reduction in recruitment to that part of the population larger than the minimum legal size (Melville-Smith et al., 1995; Goosen and Cockcroft, 1995; Cockcroft, 1997).

Adult somatic growth rates for this resource are assessed by means of a tag-recapture program. This is relatively simple because mature individuals molt only once a year, just prior to the start of the commercial fishing season, and samples of these animals can be tagged shortly before they molt. Annual growth increments can therefore be calculated from postmolt-tagged animals recaptured during the subsequent commercial fishing season. This type of tag-recapture data is routinely collected from most of the fishing grounds that are important to the South African commercial fishery (Fig. 1, inset). This tagging program has yielded one of the most comprehensive rock lobster tagging-for-growth databases in the world; it contains continuous time-series for most areas since 1986 and broken time-series for some sites dating back to the 1969–70 season (Goosen and Cockcroft, 1995). Consequently, temporal and spatial trends in adult growth are well described (Melville-Smith et al., 1995; Goosen and Cockcroft, 1995; Cockcroft, 1997; Cruywagen, 1997; Pollock et al., 1997). By contrast, little is known about what may affect juvenile growth rates.

Of particular concern is the lack of information regarding the way in which juvenile growth rates might have been affected by factors that

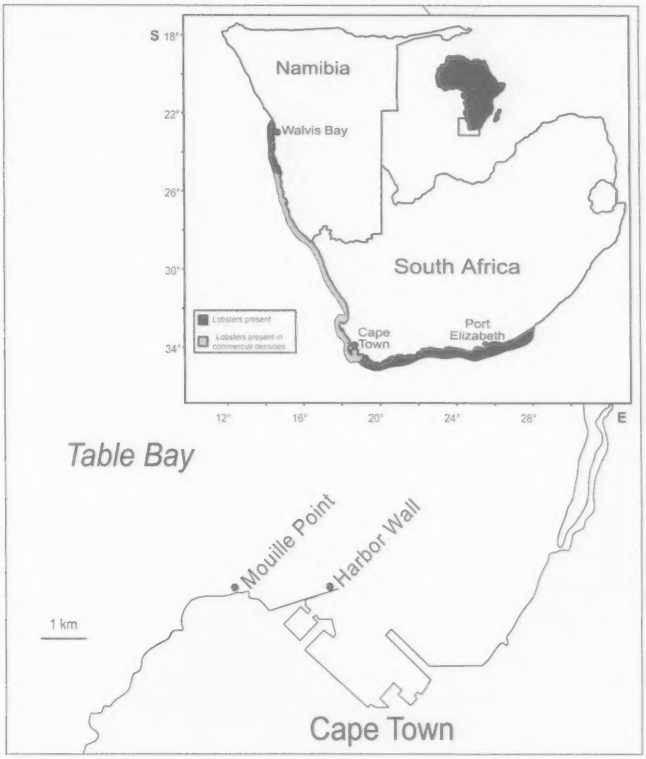

Figure 1

Map of Table Bay showing the position of the two study sites. Inset: map of southern Africa showing the distribution of rock lobster, *Jasus lalandii*.

caused the decline in adult growth rates during the early 1990s. A decrease in the size of females at 50% maturity provided indirect evidence that juvenile growth rates may also have been adversely affected (Pollock, 1987; Cockcroft and Goosen, 1995; Pollock, 1995; Pollock, 1997), but this decline in juvenile growth rates has not been confirmed by direct measurement.

Despite both this substantial gap in our knowledge of the ecology of *J. lalandii* and the growing international recognition of the importance of understanding the early life history stages of species with complex life cycles (Herrnkind et al., 1994), juvenile growth of this species was last assessed more than 25 years ago (Pollock, 1973). It was therefore essential that juvenile growth be re-examined by repeating Pollock's (1973) study at Cape Town harbor wall. This site was originally selected because of the large numbers of juvenile rock lobster present on the vertical face of the harbor wall and because these lobsters were easy to collect. In our study, a second, natural nursery reef site at nearby Mouille Point (Fig. 1) was selected to compare with the original artificial harbor wall site.

This paper addresses two hypotheses. The first is that somatic growth rates of juveniles on the harbor wall have not declined since Pollock's (1973) study. The second is that juvenile growth rates of rock lobster on the harbor wall are not different from those of rock lobster on the nearby natural nursery reef at Mouille Point.

Methods

Juvenile rock lobsters were collected between March 1996 and February 1997 at two sites: Cape Town harbor wall (seaward side) and Mouille Point (Fig. 1). Only the harbor wall was sampled in March and intervals between samples were approximately one month, although it was not possible to sample either site every month. Two autumn months (one for Mouille Point), two winter months, two spring months, and three summer months were sampled, thereby allowing for seasonal variation in growth.

Juvenile rock lobsters were sampled by two SCUBA divers who collected specimens for roughly 20–30 minutes, or by one diver for about twice as long (Table 1). At the harbor wall, divers started at the base of the wall (>10 m depth) and worked their way up to the surface, collecting every lobster encountered, where possible. At Mouille

Table 1

Summary of data relating to the field sampling of juvenile rock lobster at Mouille Point and Cape harbor wall, 1996–97.

Site	Sample date	Number of divers	Effort (diver minutes)	Water temperature[1] (°C)	Postmolt		Intermolt	Premolt		Total
					Soft new	Hard new	Hard	Hard old	Soft old	
Mouille Point	4 Apr 1996	1	40	11.2	2	4	202	65	0	273
	21 Jun 1996	1	50	13.5	2	3	167	67	0	239
	24 Jul 1996	2	30	13.3	8	15	174	56	0	253
	17 Oct 1996	2	75	12.5	2	10	239	80	4	335
	27 Nov 1996	2	50	9.4	4	12	291	58	0	365
	20 Dec 1996	1	40	10.0	4	14	212	60	1	291
	30 Jan 1997	2	50	8.8	2	19	224	52	0	297
	25 Feb 1997	2	65	9.2	5	17	176	77	0	275
Harbor wall	15 Mar 1996	1	60	10.0	12	6	325	121	0	464
	24 Apr 1996	2	55	12.5	3	7	228	52	0	290
	21 Jun 1996	1	20	13.5	1	1	210	42	2	256
	24 Jul 1996	1	45	13.3	8	13	243	29	6	299
	17 Oct 1996	2	60	12.5	3	15	205	80	0	303
	29 Nov 1996	2	45	12.9	4	9	262	30	0	305
	20 Dec 1996	1	40	10.0	6	7	275	38	0	326
	30 Jan 1997	2	50	8.8	2	13	280	38	2	335
	25 Feb 1997	2	64	9.2	10	34	210	76	0	330

[1] Temperature readings were taken from a temperature logger located in 10 m of water approximately 2 km east of Mouille Point.

Point, divers swam around the reef area, covering different habitat types (ledges, vertical walls, cracks, etc.), and attempted to catch every lobster encountered.

The catch was maintained in a bin of seawater until the sex, shell state (*sensu* Pollock, 1973) and carapace length (CL) of each animal could be recorded. Hard old and soft old shell states were considered to represent premolt animals, soft new and hard new to represent postmolts, and those animals in the hard shell state were considered to be in the intermolt phase of the molt cycle. Postmolt and intermolt specimens were released, whereas premolt animals were measured to the nearest 0.1 mm and transported to the laboratory. Whenever relatively few premolt specimens of a particular size-category were captured during routine searches, additional dive time was spent collecting these. In the laboratory, captive specimens were transferred to perforated plastic jars (either 250 or 500 cm^3 in volume, with square perforations of approximately 25 mm^2), which were placed in a 2-m^3 holding tank. To mimic natural conditions (Table 1), aquarium water temperature was controlled between 11° and 14°C during holding, with a mean of 12.6°C (SD=0.48°C), and salinity was maintained at 35–36‰ by periodic addition of freshwater or partial replacement of seawater. Stocking density did not exceed three specimens per jar, and larger specimens were held singly or in pairs. By using a combination of jar number, sex, premolt carapace length, and the pattern of missing limbs, it was possible to identify each individual. Because *J. lalandii* are unable to feed shortly before molting (Zou-tendyk, 1988), it was assumed that no feeding was required. Jars were checked for molting individuals at least every second day. Cast exoskeletons were examined to identify those molting, and each new carapace length, as well as any limb regeneration, was recorded once the shell had hardened. Increment data recorded for December 1996 were discarded because of aquarium failure: raised temperatures and lower oxygen levels resulted in high mortality during molting. Because increments from specimens maintained in the laboratory for more than 18 days were considered unreliable, only animals that molted within this period were included in analyses.

Tests of the hypothesis that somatic growth rates of juveniles on the harbor wall had not declined since Pollock's (1973) study were complicated by the absence of his original data. All that remain are mean molt increments for male and for female specimens categorized into 5-mm-CL size classes, their standard deviations, and their sample sizes. Calculation of combined mean increments for males and females of a given size is simple, but their standard deviations had to be approximated by adding corresponding sums of squares for males and females and dividing this value by the overall degrees of freedom within the size class (Table 2). It had been our intention to compare these reconstructed data with those from our study by using a two-way ANOVA (site × size class), but this was not possible, given the limitations of Pollock's (1973) data. Instead, the data were subjected to a one-way ANOVA and subsequent Student-Newman-Keuls

Table 2

Mean molt increments and their standard deviations (mm CL) of juvenile *Jasus lalandii* measured on the harbor wall in 1971–72 and 1996–97, and at Mouille Point in 1996–97.

Size class (mm CL)	Harbor wall 1971–72[1]			Harbor wall 1996–97			Mouille Point 1996–97		
	n	Mean	SD[2]	*n*	Mean	SD	*n*	Mean	SD
15–20	14	2.65	0.76	35	1.94	0.56	21	2.10	0.46
20–25	37	3.12	0.82	98	2.45	0.56	74	2.72	0.64
25–30	28	3.71	1.08	95	2.78	0.64	80	2.93	0.68
30–35	14	4.36	0.73	64	3.07	0.75	93	2.86	0.96
35–40	17	4.71	0.54	33	3.39	0.93	44	3.56	0.90
40–45	23	4.72	0.93	13	3.66	0.93	29	3.74	0.77
45–50	23	5.02	0.62	6	3.50	0.79	3	4.00	0.69

[1] After Pollock (1973).

[2] An approximation of the standard deviation calculated by adding the sums of squares for males and females, and dividing by the overall degrees of freedom.

multiple range *post hoc* tests (SigmaStat, version 2.03, [SPSS Inc., 1997]). Of greatest interest in this analysis were the results of *post hoc* tests in which means of the corresponding size classes of the two sample periods were compared.

For comparison of length-related growth increments at the two sites in our study, individual molt increments were plotted against premolt carapace lengths, for each combination of sex and site, and their linear regressions were compared by using a two-way ANCOVA (Zar, 1984; Norman and Streiner, 1994).

Investigating relative intermolt periods from field samples requires identifying those specimens that are considered to be molting. Rock lobster juveniles in the hard old shell state (*sensu* Pollock [1973]) were easily identified as such by visual inspection, and we confirmed this by breaking the tip off an antenna and inspecting the condition of the underlying integument. Furthermore, on returning these specimens to the laboratory, they generally molted within 20 days. Because field samples were taken at intervals at least this long (Table 1), the proportion of each sample found to be in the hard old shell state was a reasonable indication of the relative number of juveniles molting during that sample month. This proportion, in turn, was used as a proxy for intermolt period under the assumption that shorter intermolt periods would result in relatively higher numbers of juveniles that were molting. The numbers of specimens with soft old or soft new shells did not accurately reflect the relative rate of molting because, as a result of behavioral modifications, rock lobster in these conditions may have had a lower catchability than those with hard shells.

Using this index of relative intermolt period, we performed a log-linear analysis (Zar, 1984; Norman and Streiner, 1994) to assess the interdependence of the factors site, size-category, sample month, and molt state with regard to the frequency of observations in each subcategory. Only size classes smaller than 40 mm carapace length were used in our analysis because the decreasing molt frequency with increasing carapace length means that larger sample sizes are required to accurately estimate the proportion of animals of the size class in which rock lobsters are molting in the population. However, the length distribution of juvenile lobsters meant that sample sizes decreased above 40 mm CL.

Results

An average of 323 juvenile *J. lalandii* was collected per sample at the harbor wall (256–464), and 291 at Mouille Point (239–365). After directed collections for additional premolt specimens of various sizes, a total of 375 juveniles from the harbor wall and 383 from Mouille Point were maintained in the laboratory for analysis of growth rates. Mortality rates were low (<1%) among these specimens, except during December 1996, when aquarium malfunction resulted in extensive fatalities during molting. Cannibalism was not observed during laboratory trials.

Individual molt increments amongst the captive specimens were highly variable, ranging from 0.4 to 5.5 mm. However, mean molt increments for each of seven consecutive 5-mm-CL size-intervals (Table 2) were consistently and significantly smaller in our study (1996–97 season) than those measured in 1971–72 (Table 3, Fig. 2). Thus, the hypothesis that somatic growth rates of juveniles on the harbor wall had not declined since Pollock's (1973) study could be rejected at one level. Unfortunately, there were no comparative data to provide accurate information on corresponding intermolt periods.

In terms of our samples from Mouille Point and the harbor wall, significant, positive linear relationships were found between molt increment and premolt carapace length for both males and females at both sites (Fig. 2,

Table 3

Results of one-way ANOVA comparing growth increments among size-intervals at the harbor wall from the two sample periods. Subsequent *post hoc* Student-Newman-Keuls multiple-range test results are summarized in the matrix below; an asterisk indicates that molt increments differ significantly ($P<0.05$) between the two samples being compared.

Source of variation	df	SS	MS	F	P
Between groups	13	332.57	25.58	48.1	<0.001
Within groups	486	258.48	0.53		
Total	499	591.06			

		1971–72							1996–97						
	Size class (mm CL)	15–20	20–25	25–30	30–35	35–40	40–45	45–50	15–20	20–25	25–30	30–35	35–40	40–45	45–50
1971–72	15–20			*	*	*	*	*	*					*	
	20–25			*	*	*	*	*	*	*					
	25–30	*	*			*	*	*	*	*	*	*		*	
	30–35	*	*			*	*	*	*	*	*	*	*	*	
	35–40	*	*	*	*		*	*	*	*	*	*	*	*	*
	40–45	*	*	*	*	*			*	*	*	*	*	*	*
	45–50	*	*	*	*	*			*	*	*	*	*	*	*
1996–97	15–20	*	*	*	*	*	*	*		*	*	*	*	*	*
	20–25		*	*	*	*	*	*	*		*	*	*	*	*
	25–30			*	*	*	*	*	*	*				*	
	30–35			*	*	*	*	*	*	*					
	35–40				*	*	*	*	*	*					
	40–45	*		*	*	*	*	*	*	*	*				
	45–50					*	*	*	*	*					

$P<0.0001$ in all cases). Three females at the harbor wall >50 mm CL were excluded from all analyses (unshaded circles, Fig. 2A) because they were the only specimens of this size. Further, females >50 mm CL might have had smaller than expected molt increments due to approaching maturity (Pollock, 1973).

Two-way, fixed effects ANCOVA comparing these linear regressions indicated no interaction between the factors site and sex; nor was there a significant sex-effect (Table 4). However, there was a significant site-effect: the relationship for samples from Mouille Point had a significantly higher regression constant than that for samples from the harbor wall (Table 4). These results imply first that there were no differences in length-specific growth increments between the sexes within sites. The second implication is that molt increment increased with carapace length at the same rate, irrespective of sex or site. Finally, juvenile lobsters of any given size or sex at Mouille Point grew significantly more during each molt stage than corresponding specimens at the harbor wall (see also Table 2 and Fig. 2).

Log-linear analysis indicated significant first-, second-, and third-order interactions among the factors site, size-category, sample month, and molt state (Table 5). However, the only significant third-order interaction was that among the independent factors site, size-category, and sample month. This interaction simply confirmed that size-frequency distributions differed between sites over the sample period, as would be expected if growth rates differed. Of the three remaining nonsignificant third-order interactions, the most important for our purposes were those including the site factor. These imply that the temporal pattern of molting is similar between sites, as is the size-specific pattern of molting. These results are supported by graphical representations of the data (Fig. 3), which suggest that for both sites 1) the proportion of molters per size-category decreases as size increases, and 2)

Table 4

Summary of ANCOVA results from length-specific molt increments classified according to sex and site.

Factor	df_{effect}	df_{error}	F	P
Slope				
Site	1	597	0.70	0.40
Sex	1	597	0.66	0.42
Site × sex	3	595	0.61	0.61
Elevation				
Site	1	598	4.63	0.03
Sex	1	598	1.11	0.29
Site × sex	1	598	0.01	0.93

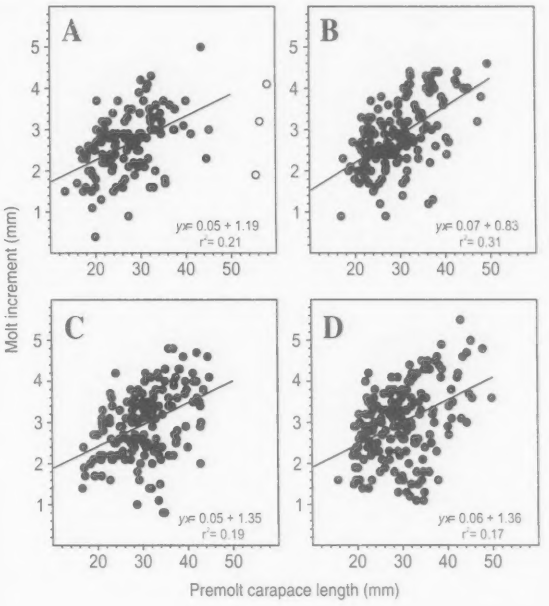

Figure 2

Relationship between molt increment and premolt carapace length of juvenile lobsters at the harbor wall and Mouille Point: (**A**) harbor wall females, (**B**) harbor wall males, (**C**) Mouille Point females, (**D**) Mouille Point males. Shaded circles represent data included in analyses; unshaded circles represent data excluded from analyses (see text for details).

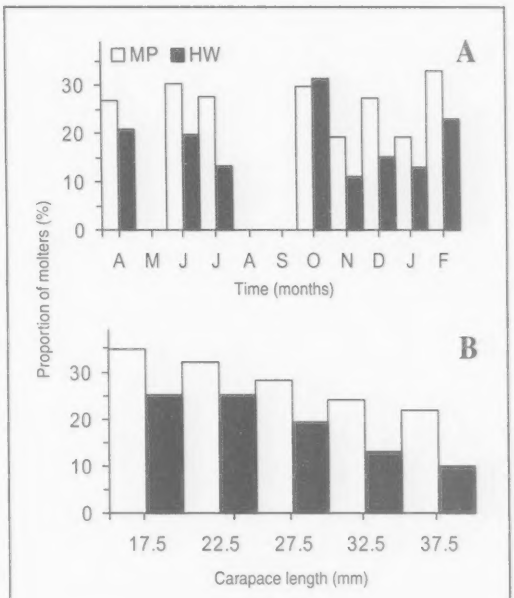

Figure 3

Site-specific patterns of the proportions of sampled juvenile rock lobster that were considered to be molting with respect to (**A**) sample month and (**B**) 5-mm-CL size classes. MP = Mouille Point; HW = harbor wall.

the proportion of lobsters in the molt state fluctuates over time. In both cases, the proportion of lobsters in the molt state was consistently lower at the harbor wall than at Mouille Point (with the exception of the sample taken in October 1996). This apparent dependence of molt state on each of the factors site, size-category, and sample date is confirmed by the corresponding significant second-order interactions (Table 5).

Together with the molt-increment data, these results give reason to reject the hypothesis that current juvenile growth rates on the harbor wall are no different from those on the nearby natural nursery reef in Mouille Point; growth is significantly faster at the latter.

Discussion

The significance of puerulus and postpuerulus ecology to the management of rock lobster fisheries is now widely accepted (Herrnkind et al., 1994). In the South African *J. lalandii* resource, the current controversy surrounding the question of whether or not temporal trends in juvenile growth rates reflect those of adults provides a good example of why so much emphasis should be placed on early life history stages. For this species, adult somatic growth rates have declined substantially since the mid-1980s (Melville-Smith et al., 1995; Cockcroft, 1997, Cockcroft and Payne, 1999). Although the causes of this phenomenon are not yet clearly understood, its widespread nature is indicative of a large-scale environmental perturbation. This has prompted hypotheses that the anomalous *El Niño* years of 1990–93 may have resulted in dramatic changes in the productivity of the southern Benguela Current (Pollock et al., 1997; Pollock et al., 2000). Alternatively, it is plausible that heavy, size-selective fishing of this resource may have caused a decline in growth rates by removing individuals genetically predisposed to more rapid growth (see for example Stokes and Law [2000]). Notwithstanding the causes, if it is incorrectly assumed that juvenile growth rates mirror the trends of the regularly monitored adults, overly conservative estimates of recruitment into the fishery might result, whereas assuming the converse could lead to a higher risk of overfishing.

Results from our re-examination of the growth rates of juvenile *J. lalandii* provided some evidence that temporal trends in their growth rates are consistent with those of the adults of the species. Specifically, juvenile molt increments at the Cape Town harbor wall were smaller in

Table 5

Results of log-linear analysis investigating the interdependence of the factors site (S), size-category (SC), sample month (M) and molt state (MS) with regard to the frequency of observations in each subcategory. χ^2 statistics are reported for conventional tests of observed versus expected frequencies and have been calculated for model fits with different numbers of levels of interactions as well as for partial and marginal associations among combinations of factors. In the latter sense, partial associations take into account the effect of all factors at each given level, whereas marginal associations take into account only those factors listed (Norman and Streiner, 1994).

Tests of hypotheses that all *K*-level interactions are simultaneously zero.

Level (*K*)	df	χ^2	*P*
1	13	1833.48	< 0.01
2	51	626.90	< 0.01
3	67	168.45	< 0.01
4	28	39.51	0.07

Tests of marginal and partial association

		Partial association		Marginal association	
Factor	df	χ^2	*P*	χ^2	*P*
Site (S)	1	6.60	0.01		
Size-category (SC)	4	500.95	< 0.01		
Sample month (M)	7	42.78	< 0.01		
Molt state (MS)	1	1198.48	< 0.01		
$S \times SC$	4	142.77	< 0.01	125.72	< 0.01
$S \times M$	7	23.89	< 0.01	21.05	< 0.01
$S \times MS$	1	52.47	< 0.01	35.73	< 0.01
$SC \times M$	28	320.55	< 0.01	307.70	< 0.01
$SC \times MS$	4	68.53	< 0.01	41.78	< 0.01
$M \times MS$	7	68.24	< 0.01	55.70	< 0.01
$S \times SC \times M$	28	121.80	< 0.01	129.12	< 0.01
$S \times SC \times MS$	4	7.99	0.09	4.91	0.30
$S \times M \times MS$	7	16.04	0.03	11.51	0.12
$SC \times M \times MS$	28	28.66	0.43	32.55	0.25

1996–97 than those recorded in 1971–72 (Pollock, 1973), irrespective of size. Although corresponding measures of intermolt period are not available, established trends in juvenile rock lobster biology indicate that such data would probably not have exhibited conflicting trends. In general, their growth rates tend to respond first by changes in molt frequency and then, under more extreme conditions, by changes in molt increments (Chittleborough, 1975; Serfling and Ford, 1975; Phillips et al., 1977; Dennis et al., 1997). Therefore, the trend to smaller growth increments among juvenile *J. lalandii* at the Cape Town harbor wall between 1971–72 and 1996–97 was most plausibly accompanied by an increase in intermolt period.

Adding credence to this deduction are Cockcroft and Goosen's (1995) results, which demonstrated that the size at which female *J. lalandii* reach sexual maturity on a range of fishing grounds had decreased significantly over the two decades leading up to the mid-1990s. Using simulation models, Pollock (1987) demonstrated that reduced juvenile growth rates would lead to a smaller size at sexual maturity. In combination, these conclusions provided additional rationale for rejecting the hypothesis that somatic growth rates of juvenile *J. lalandii* on the harbor wall have not declined since the last study.

Pollock (1973) found that a modal size of 38 mm CL was attained approximately 1.6 years after settling. This alone implies a slower growth rate than that for other temperate lobster species (Jernakoff et al., 1994). Because our data suggest that current growth rates are even slower than this, and that they may decline further with falling adult growth rates, recruitment to the fishable part of the *J. lalandii* resource must be seen as a real management concern (Bergh and Johnston, 1992). Therefore, the precautionary assumption made in the operational management procedure designed for this resource (Cockcroft and Payne, 1999; Pollock et al., 2000) that juvenile growth mirrors adult growth is justified.

Another feature of trends in growth rates shared between adult and juvenile *J. lalandii* is small-scale spatial variation. During the monitoring period, juveniles of this species grew relatively faster at Mouille Point than at the harbor wall, both in terms of molt increment

and intermolt period. Amongst adults, this variability has been attributed to patterns of food availability and gradients in environmental characteristics, particularly oxygen content (Newman and Pollock, 1974; Pollock and Beyers, 1981; Pollock, 1982; Pollock and Shannon, 1987; Pollock et al., 1997; Mayfield, 1998). Although there is some spatial separation of juvenile and adult *J. lalandii*, it is likely that the biotic structure of their environment influences juvenile growth rates in a manner similar to that of adults.

In a study of the diets of juvenile lobsters at the Cape Town harbor wall and Mouille Point, Mayfield (1998) found that diets were similar at the two sites, but that the benthic communities differed. He concluded that lobsters on the harbor wall would have to spend more time and energy feeding to maintain a diet similar to those at Mouille Point, where more favored food species (e.g. mussels, barnacles) were better represented. Similar patterns were evident when comparing diets of adults at Olifantsbos and Dassen Island (Mayfield, 1998), a slow- and fast-growth site, respectively (Cockcroft and Goosen, 1995). Subsequently, a more detailed study of the diets of two size classes (<35 mm CL and 40–60 mm CL) of juvenile *J. lalandii* at the Cape Town harbor wall and at Mouille Point was able to detect a significant difference between the diets of inhabitants of the two sites (Mayfield et al., 2000). Juveniles on the harbor wall consumed significantly less black mussel, their preferred prey species. This result, however, does not contradict the suggested link between food distribution and juvenile growth rates; specimens forced to subsist off suboptimal food resources could be expected to grow more slowly than those at liberty to pursue their preferred prey.

The differences in growth rates between juvenile *J. lalandii* at the artificial harbor wall and those at the natural nursery reef at Mouille Point do not necessarily preclude the use of the harbor wall as a legitimate site to continue monitoring juvenile growth. The existence of historical data (albeit for only two seasons) provides a good reference point, and the easy and consistent sampling conditions permit reliable data collection. These sampling conditions are of particular importance, given the established tendencies of early juveniles of other species of rock lobster on natural reefs to be less vulnerable to sampling than later stages (Annala and Bycroft, 1985; Marx and Herrnkind, 1985; Breen and Booth, 1989; Jernakoff, 1990; Childress and Herrnkind, 1994; Forcucci et al., 1994; Jernakoff et al., 1994). Furthermore, knowledge of how growth rates change over time is in itself important to the management of the fishery (Cockcroft, 1997).

Should spatial and temporal variability in juvenile growth continue to be a contentious issue, a juvenile tagging program would provide simpler and more rigorous comparisons. It might also provide reliable estimates of the intermolt period. Mitigating against this, however, are the low rate of recapture of tagged specimens in the wild and potential tag-related growth retardation and mortality. Nevertheless, continued monitoring of juvenile growth may elucidate how close this link is between adult and juvenile growth, thereby improving our ability to manage this valuable resource.

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Stock-rebuilding time isopleths and constant-*F* stock-rebuilding plans for overfished stocks

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Abstract–Stock-rebuilding time isopleths relate constant levels of fishing mortality (F), stock biomass, and management goals to rebuilding times for overfished stocks. We used simulation models with uncertainty about F_{MSY} and variability in annual intrinsic growth rates (r_y) to calculate rebuilding time isopleths for Georges Bank yellowtail flounder, *Limanda ferruginea*, and cowcod rockfish, *Sebastes levis*, in the Southern California Bight. Stock-rebuilding time distributions from stochastic models were variable and right-skewed, indicating that rebuilding may take less or substantially more time than expected. The probability of long rebuilding times increased with lower biomass, higher F, uncertainty about F_{MSY}, and autocorrelation in r_y values. Uncertainty about F_{MSY} had the greatest effect on rebuilding times. Median recovery times from simulations were insensitive to model assumptions about uncertainty and variability, suggesting that median recovery times should be considered in rebuilding plans. Isopleths calculated in previous studies by deterministic models approximate median, rather than mean, rebuilding times. Stochastic models allow managers to specify and evaluate the risk (measured as a probability) of not achieving a rebuilding goal according to schedule. Rebuilding time isopleths can be used for stocks with a range of life histories and can be based on any type of population dynamics model. They are directly applicable with constant F rebuilding plans but are also useful in other cases. We used new algorithms for simulating autocorrelated process errors from a gamma distribution and evaluated sensitivity to statistical distributions assumed for r_y. Uncertainty about current biomass and fishing mortality rates can be considered with rebuilding time isopleths in evaluating and designing constant-F rebuilding plans.

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Stock-rebuilding plans proposed for overfished stocks are best evaluated by stock-specific simulation analysis (e.g. PFMC[1]). However, general approaches are also valuable because many stocks are overfished (NMFS, 1999) and default or generic rebuilding plans can be used without extensive analyses for each species (e.g. PFMC[2]; Applegate et al.[3]). In this article we show how stock-rebuilding time isopleths can be used to design, evaluate, and monitor progress of "constant F" and other types of rebuilding plans. Constant-F stock-rebuilding plans maintain fishing mortality at a fixed level until the stock is rebuilt, and are relatively simple and easy to analyze. The isopleth approach is easy to use as both a general and stock-specific tool.

The U.S. Sustainable Fisheries Act (SFA) mandates rebuilding plans for overfished stocks (DOC, 1996, 1998). Federally managed stocks are considered overfished when stock biomass is less than the biomass threshold ($B_{Threshold}$) defined in the Fishery Management Plan (FMP). National Standard 1 (DOC, 1998) for the SFA indicates that $B_{Threshold}$ should be the greater of one-half of B_{MSY} (the theoretical biomass level for maximum sustained yield, MSY) or the minimum biomass from which rebuilding to B_{MSY} could be expected to occur within ten years if the stock is exploited at $F_{Threshold}$. Typically, $F_{Threshold} = F_{MSY}$ (the theoretical fishing mortality rate for MSY) when current biomass is at or above $B_{Threshold}$, and $F_{Threshold} < F_{MSY}$ at lower biomass levels. A common approach (Fig. 1, and Thompson, 1999) reduces $F_{Threshold}$ from the F_{MSY} level linearly to zero as biomass declines from $B_{Threshold}$. In cases where B_{MSY} and F_{MSY} can not be estimated, reasonable proxy values (e.g. one-half unfished biomass or $F_{0.1}$) are typically used instead.

The goal for most rebuilding plans under the SFA is to achieve the target biomass level (B_{MSY} or an acceptable proxy level) in ten years or less. Even with zero fishing mortality, ten years may not be sufficient to rebuild some overfished stocks. In such cases, the Guidelines for National Standard 1 allow a rebuilding time period no longer than one mean generation time (Restrepo et al., 1998) plus the expected time to recovery in the absence of fishing mortality (DOC, 1998).

[1] PFMC (Pacific Fishery Management Council). 1999. The coastal pelagic species fishery management plan, Amendment 8, 405 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR, 97220-1384.

[2] PFMC (Pacific Fishery Management Council). 1999. Status of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catch for 2000 stock assessment and fishery evaluation, 230 p. Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR, 97220-1384.

[3] Applegate, A., S. Cadrin, J. Hoenig, C. Moore, S. Murawski, and E. Pikitch. 1998. Evaluation of existing overfishing definitions and recommendations for new overfishing definitions to comply with the Sustainable Fisheries Act, 179 p. New England Fishery Management Council, 50 Water Street, Mill 2, Newburyport, MA 01950.

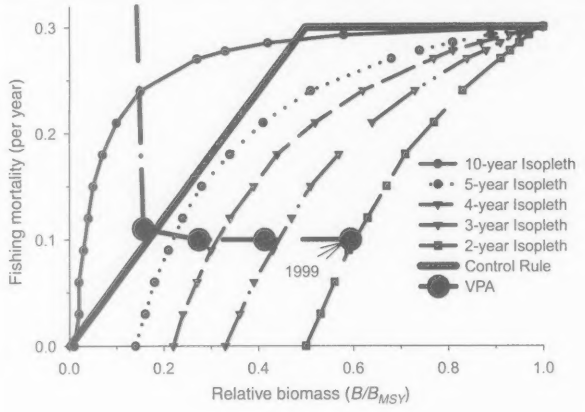

Figure 1

Isopleths for median rebuilding times based on a deterministic logistic population growth model (model type 1) for Georges Bank yellowtail flounder with F_{MSY}=0.3. Also shown are a common harvest control rule, and the biomass-F trajectory during 1996–99 for Georges Bank yellowtail flounder. The harvest control rule specifies a maximum (threshold) F as a function of stock biomass level. The biomass-F trajectory shows a time series of F and biomass estimates from virtual population analysis (VPA, Cadrin[5]).

Stock-rebuilding time isopleths

Cadrin (1999) calculated theoretical recovery times for Georges Bank yellowtail flounder (*Limanda ferruginea*) and used rebuilding time isopleths to depict trends in stock biomass in relation to fishing mortality. Calculations were based on a deterministic logistic population growth model with a range of constant annual fishing mortality rates ($\bar{F}$=zero to F_{MSY}) and a range of initial biomass levels less than the target level (B_0=zero to B_{MSY}). Recovery time was the number of years required for stock biomass to increase from an initial overfished biomass level ($B_0<B_{Threshold}$) to the biomass target $B_{Target}=B_{MSY}$, assuming a constant annual fishing mortality rate. Rebuilding time isopleths were formed by connecting points of initial biomass and constant fishing mortality (B_0, $\bar{F}_{B_0}$) with the same recovery time (Fig. 1). For example, beginning at the initial biomass level $B_0<B_{Target}$, any constant fishing mortality rate $\bar{F}_{B_0}$ on the 10-year isopleth would theoretically rebuild the stock to B_{Target} in ten years. In contrast, any constant-F value $<\bar{F}_{B_0}$ (below or to the right of the isopleth) would rebuild the stock sooner and any constant F values $>\bar{F}_{B_0}$ (above or to the left of the isopleth) would rebuild the stock later. Rebuilding time isopleths were used to develop overfishing definition options for nine overfished New England groundfish stocks (Applegate et al.[3]).

In this article, we calculate stock-rebuilding time isopleths based on stochastic population dynamics models and characterize statistical distributions (mean, median, and percentiles) of stock-rebuilding times under different assumptions about uncertainty and process error (process errors are uncertainty in population dynamics due to natural variability in growth, recruitment, and other biological factors, Hilborn and Walters, 1992). Like Cadrin (1999), we use logistic population growth models, but our analysis includes uncertainty about F_{MSY} and autocorrelated process errors in production. We analyze rebuilding times for two stocks (cowcod rockfish, *Sebastes levis*, and Georges Bank yellowtail flounder) with different life histories, levels of F_{MSY}, and autocorrelation in production process errors (the calculations are examples only and not for use by managers). We also describe how stock-rebuilding time isopleths from deterministic and stochastic models can be used to develop and evaluate rebuilding plans and to monitor their progress.

Materials and methods

Following Prager (1994), we used the continuous time version of the logistic population dynamic model in simulation calculations.[4] In particular, for the logistic population growth parameter r_y (subscripted to represent the value in year y) carrying capacity K, $b_y = r_y / K$, and $a_y = r_y - F_y \neq 0$:

$$B_{y+1} = \frac{a_y B_y e^{a_y}}{a_y + b_y B_y (e^{a_y} - 1)}. \quad (1)$$

[4] SAS simulation program code available from the senior author.

Table 1

Six types of simulation models used to estimate rebuilding time isopleths. Model types include all of the meaningful combinations of uncertainty about F_{MSY} and variance and autocorrelation in production process errors.

Model type	CV for uncertainty in F_{MSY} (%)	Variance in process errors (%)	Autocorrelation in process errors (ρ)	Description
1	Zero	0	zero	No uncertainty about F_{MSY}; deterministic production
2	20	0	zero	Uncertainty about F_{MSY}; deterministic production
3	Zero	from stock assessment	zero	No uncertainty about F_{MSY}; stochastic production; no autocorrelation
4	20	from stock assessment	zero	Uncertainty about F_{MSY}; stochastic production; no autocorrelation
5	Zero	from stock assessment	from stock assessment	No uncertainty about F_{MSY}; stochastic production; with autocorrelation
6	20	From stock assessment	from stock assessment	Uncertainty about F_{MSy}; stochastic production; with autocorrelation

When fishing and the intrinsic rate of increase exactly balance ($a_y = r_y - F_y = 0$):

$$B_{y+1} = \frac{B_y}{1 + b_y B_y}. \quad (2)$$

Note that biomass declines ($B_{y+1} < B_y$) when $r_y - F_y = 0$ because r_y is a maximum value defined in the limit as biomass approaches zero (Eq. 1).

Following Beddington and May (1977) and May et al. (1978), natural variation in population growth rates was included in our analysis by adding process errors to simulated r_y values. We hypothesized that the intrinsic rate of population increase was more important than carrying capacity in simulating population growth rates at low biomass levels, and in rebuilding overfished stocks. We focused on stochastic variation in r_y because it likely varies annually (e.g. due to variation in recruitment and growth). We could hypothesize reasonable lower bounds which included negative values; and variability in r_y could be reasonably described in statistical terms (e.g. mean, variance, and autocorrelation) based on available data. Carrying capacity (K) was assumed constant over time because no information about potential covariance in r_y and K was available.

In the deterministic logistic population model, $F_{MSY} = r/2$ and $B_{MSY} = K/2$ (Schaefer, 1954). For the sake of simplicity, we assumed $K = 1$ so that $B_{Target} = B_{MSY} = 0.5$ and biomass B_y was measured in relation to K (e.g. $B_y = K = 1$ at carrying capacity). It was useful to express biomass in relation to K because estimates of ratios like B_t/B_{MSY} ($= 2B_t/K$) are often more precisely estimated than either biomass B_y or carrying capacity K (Prager, 1994) and because the approach makes results easier to apply to other stocks.

We used six types of logistic population growth models (Table 1) based on a wide range of initial biomass (B_0), two levels of uncertainty about F_{MSY}, variance in process errors (stock dependent), and autocorrelation in process errors (also stock dependent). The number of years (an integer) required for the stock to rebuild to $0.95B_{MSY}$ was recorded in each simulation run. Recovery in the simulation model was at $0.95B_{MSY}$, rather than B_{MSY}, because biomass in the deterministic logistic production model at $F = F_{MSY}$ approaches asymptotically (but never reaches) B_{MSY} (this convention had negligible effect on results). Stochastic simulation model results were derived from 2000 individual model runs (the maximum length of each run was 2000 years) starting from each point in a grid of 31 values of F (i.e. 0, $F_{MSY}/30$, $2F_{MSY}/30$, ..., $29F_{MSY}/30$, F_{MSY}) and 35 values of initial biomass (i.e. $B_0 = 0$, $\delta \times 10^{-3}$, $\delta \times 10^{-2}$, $\delta \times 10^{-1}$, δ, 2δ, ..., 30δ, where $\delta = 0.9999 \times 0.95 \times B_{MSY}/K/30$).

We calculated distributional statistics including the mean, median ($Q_{50\%}$), and various quantiles (e.g. $Q_{90\%}$ for the ninety-percent quantile) for recovery times from all runs at each point in the grid of F and initial biomass levels. We then plotted isopleths (contours) for the distributional statistics. For example, to produce 10-year median rebuilding time isopleths, we calculated median recovery times for each point in the grid of F and initial biomass, and then drew contours (isopleths) by connecting points with 10 year median rebuilding times to identify fishing mortality rates that, if held constant, would give a 50% probability of rebuilding from the initial biomass to the target in ten years. We smoothed the isopleths in plots by using LOESS (locally weighted regression smoothing) regression (Cleveland and Devlin, 1988; Cleveland et al., 1988) to remove variation caused by the contouring algorithm and coarse grid of fishing mortality and biomass starting points.

Uncertainty

Uncertainty in estimates of F_{MSY} is likely larger than typically measured by variance estimates in assessment models because uncertainties in catch, the assumed natural mortality rate, somatic growth, and other factors are generally not included in stock assessment model variance calculations. In simulation runs including uncertainty, we used

$$F_{MSY,s} = \hat{F}_{MSY} + \varepsilon_s, \quad (3)$$

where $F_{MSY,s}$ was used in simulation s, $\hat{F}_{MSY}$ was the "best" estimate, and ε_s was drawn from a normal distribution with mean zero and variance $\sigma_\varepsilon^2 = \mathrm{CV}^2 \hat{F}_{MSY}^2$. The CV (20%) assumed in our simulation runs implies that the true F_{MSY} is within ±40% of the best estimate with about 95% probability. We truncated $F_{MSY,r}$ values at ±50% $\hat{F}_{MSY}$ to avoid implausibly small (including negative) or large $F_{MSY,r}$ values. These *ad hoc* bounds seemed reasonable because they were slightly larger than the 95% confidence interval implied by the CV for uncertainty (±40%).

Our assumptions about uncertainty in F_{MSY} are crude but seem reasonable based on our experience and by analogy to uncertainty about natural mortality rates (M), which are sometimes used as a proxy for F_{MSY} (Clark, 1991). In assessment work, a stock with an assumed natural mortality rate M=0.2/yr, for example, might have a "subjective" uncertainty range of about ±40% (i.e 0.12–0.28/yr). It seems reasonable to assume that uncertainty about M and F_{MSY} would be similar.

Process errors

We modeled process errors as potentially autocorrelated random changes in the intrinsic population growth parameter (r_y). Previous analyses used independent or autocorrelated random errors in realized annual production rates (dB_y/dy, Sissenwine, 1977; Gleit, 1978; Shepherd and Horwood, 1980; Ludwig, 1981; Sissenwine et al., 1988), or independent random errors in recruitment (e.g. Getz, 1984), next year's biomass (B_{t+1}, Ludwig et al., 1988), or surplus production (Doubleday, 1976). Production process errors may be independent in some cases but were autocorrelated for both of our example stocks (see "Results" section).

Our analysis, like Sissenwine et al.'s (1988), includes autocorrelated errors because they affected rebuilding times in preliminary model runs, are biologically plausible and widely recognized (favorable and unfavorable conditions for production seem to persist for more than one year in many stocks), and because correlated errors were obvious in production model fits for Georges Bank yellowtail flounder and cowcod rockfish. In contrast to previous studies, we estimated variances and autocorrelations for stochastic r_y values in our simulation models from available data. In addition, our simulation models used lower bounds for r_y based on the natural mortality rate.

We used the gamma distribution (Johnson et al., 1994, Appendix 1) to describe process errors in the production model because it is flexible, asymmetrical (like our estimates of production process errors for cowcod rockfish), and (in the three-parameter form) accommodates negative r_y values. We devised a simple way to simulate autocorrelated process errors from a distribution nearly identical to a gamma distribution used to simulate uncorrelated process errors. This makes comparisons between runs with and without autocorrelation easier. Sissenwine et al. (1988) also used a gamma distribution for production process errors because simulated state variables in logistic models (with constant catch and Gaussian process errors on the realized production rate dB_y/dy) have distributions that resemble a gamma distribution (Dennis and Patil, 1984).

The first step in modeling production process errors was to obtain empirical estimates of variance and autocorrelation. Based on stock assessment results, surplus production in each year (P_y) was computed with the following equation:

$$P_{y+1} = B_{y+1} - B_y + C_y, \quad (4)$$

where C_y = catch data was catch; and
B_y = estimated biomass at the beginning of year y.

The discrete time version of our logistic model with process errors is

$$P_y = r_y B_y \left(1 - \frac{B_y}{K}\right). \quad (5)$$

Solving for r_y gives

$$r_y = \frac{P_y K}{B_y (K - B_y)}, \quad (6)$$

where B_y should be no larger than, say, 95% K to avoid unrealistic values of r_y that are calculated when positive production is observed in stock assessment results at biomass levels near or above estimates of K. As shown in the "Results" section, empirical estimates of variance σ^2 and autocorrelation (ρ) for r_y values were relatively insensitive to assumptions about K. The variance of observed r_y values includes both process and measurement errors and is an upper bound estimate for the variance due to process errors only. In other words, results of our simulation analyses may overstate the importance of production process errors in rebuilding overfished stocks because our variance estimates may be too large.

We used $-M$ (where M is the instantaneous natural mortality rate assumed in the stock assessment) as a lower bound on r_y in simulations. Negative r_y values are common in some stocks (e.g. 36% and 17% of years for anchovies [*Engraulis* spp.] and sardines [*Sardinops* and *Sardina* spp.], Jacobson et al., 2001) because stocks can decrease in biomass from one year to next with no fishing and because negative values are occasionally seen in real data sets (e.g. Myers et al., 1999). If process errors are ignored and M is constant, then

Table 2

Summary statistics and gamma distribution parameters for annual process errors in the intrinsic population growth rate (r_y) for Georges Bank yellowtail flounder (*Limanda ferruginea*), estimated from stock assessment results (Cadrin[5] in the main text). Parameters α and β were estimated with fixed $\gamma = -M$ by maximum likelihood. According to Cadrin,[5] the carrying capacity is K=99,000 metric tons (t) (95% confidence interval 84,500–103,000 t).

Parameter	K=84,500 t	K=99,400 t	K=103,000 t
Number B_y values ≤95% K	25	25	25
Sample mean	0.58	0.65	0.58
Sample variance	0.036	0.037	0.036
Autocorrelation ρ	0.34	0.33	0.34
α	15.7	17.5	15.7
β	0.0498	0.0488	0.0499
$\gamma = -M$	–0.2	–0.2	–0.2
Mean	0.58	0.65	0.58
Variance	0.039	0.039	0.039
Mode	0.53	0.61	0.53

$$r_y = G_y + R_y - M \quad (7)$$

where G_y = the instantaneous rate of somatic growth; and
R_y = an instantaneous rate for recruitment (in units of biomass).

Somatic growth and recruitment may be density dependent but are usually positive ($G_y \geq 0$ and $R_y \geq 0$). Thus, $r_y = -M$ is possible in the extreme case of zero growth and zero recruitment.

Production process errors were simulated by drawing random numbers from a three-parameter gamma probability distribution (Johnson et al., 1994, Appendix 1). Runs with autocorrelated process errors used one of two algorithms based on gamma distributions with adjusted parameter estimates (Appendix 2).

Georges Bank yellowtail flounder

Cadrin[5] used virtual population analysis (VPA, calibrated by using survey data) to estimate stock biomass for Georges Bank yellowtail flounder during 1973–98. In the same assessment, a surplus production model (ASPIC [stock-production model incorporating covariates], Prager, 1994) was used to estimate K=93,700 metric tons (t) (80% bootstrap confidence interval 87,700–97,000 t) and F_{MSY}=0.30/yr (80% bootstrap confidence interval 0.27–0.32/yr).

Cadrin's stock assessment[5] and our production calculations indicate that Georges Bank yellowtail flounder is a moderately long-lived (maximum observed age 14 yr, assumed M=0.2 /yr), relatively productive ($\bar{r}$=0.58–0.65) stock with some autocorrelation (ρ=0.33–0.34) in production process errors (Table 2). Empirical, and gamma distributions fit by maximum likelihood and the method of moments had similar means and variances (Table 2). Surplus production and biomass are related for Georges Bank yellowtail flounder, with P_y reduced at the low B_y levels (Fig. 2A). Variability in estimated r_y values indicate autocorrelation in process errors (Fig. 2B). The distribution of r_y values (Fig. 2C) was skewed to the left and there were no negative values. Gamma distributions fitted by maximum likelihood and the method of moments (Appendix 1) were similar in shape (Fig. 2C). In simulations for yellowtail flounder, we used F_{MSY}=0.30 (from ASPIC) with $\sigma^2_{r_y}$=0.037 and ρ=0.33.

Cowcod rockfish

Butler et al.[6] (see also Butler et al.[7]) estimated K=3400 t (95% CI 2800–4000 t) with a delay-difference biomass dynamic model for cowcod rockfish in the Southern California Bight. Annual biomass estimates from the same source were used to calculate surplus production during 1951–97 when the stock was fished down from about 3200 t to 240 t (about 7% of virgin biomass).

Butler et al.[6] and our production calculations indicate that cowcod rockfish are a long-lived (maximum observed

[5] Cadrin, S. X. 2000. Georges Bank yellowtail flounder. *In* Northern demersal working group: assessment of 11 northeast groundfish stocks through 1999. *In* Northeast Fisheries Science Center Reference Document 00-05, p. 45–64. Northeast Fisheries Science Center 166 Water Street, Woods Hole, MA, 02543.

[6] Butler, J. L., L. D. Jacobson, J. T. Barnes, and H. G. Moser. 2002. Manuscript in revew. Biology and population dynamics of cowcod rockfish (*Sebastes levis*) in the southern California Bight.

[7] Butler, J. L., L. D. Jacobson, J. T. Barnes, H. G. Moser, and R. Collins. 1999. Stock assessment of cowcod. *In* Appendix to the state of the Pacific Coast groundfish fishery through 1999 and recommended acceptable biological catch for 2000 stock assessment and fishery evaluation, p. Vi–113 (section 5). Pacific Fishery Management Council, 7700 NE Ambassador Place, Portland, OR, 97220-1384.

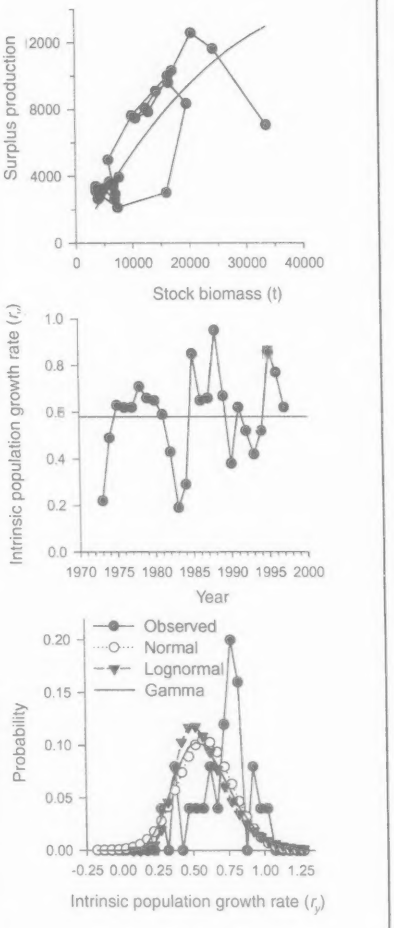

Figure 2

(**A**) Surplus production estimates P_y and biomass estimates B_y for Georges Bank yellowtail flounder during 1973–97. The biomass estimates and parabolic curve fitted to production estimates are from Cadrin.[5] (**B**) Time series of annual intrinsic rate of growth (r_y) parameter value estimates from Equation 6. (**C**) Probability distributions for r_y values used in simulations for Georges Bank yellowtail flounder.

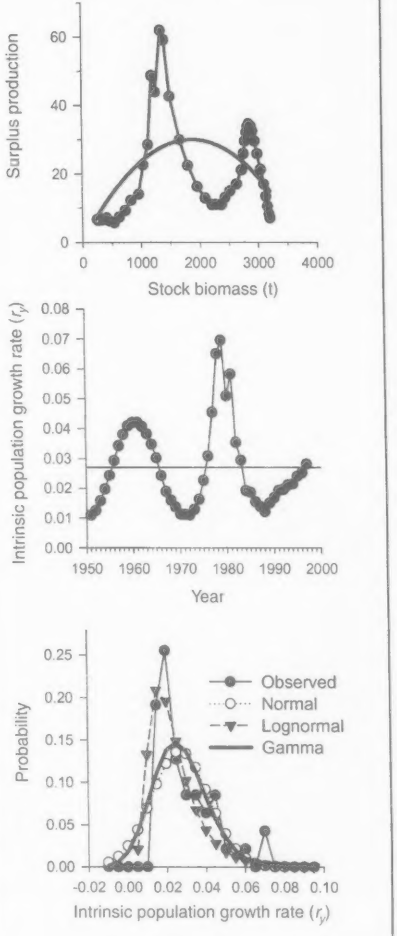

Figure 3

(**A**) Surplus production estimates P_y and biomass estimates B_y from Butler et al.[6] for cowcod rockfish during 1951–97 in the Southern California Bight. The parabolic curve fitted to production estimates (P_y) shows trends only and is not recommended for management purposes. (**B**) Time series of annual intrinsic rate of growth (r_y) parameter value estimates from Equation 6. (**C**) Probability distributions for r_y values used in simulations for cowcod rockfish.

age 55 yr, assumed M=0.055/yr), relatively unproductive stock ($\bar{r}_y$=0.027–0.037). Cowcod rockfish are much less productive than Georges Bank yellowtail flounder because of their long lives and slower growth and because adult habitat is limited to steep rocky areas in relatively deep water (90–500 m, Butler et al.[6]). Production process errors show a high level of autocorrelation (ρ=0.83–0.94, Table 3). Means, variances and autocorrelations for r_y were not very sensitive to assumptions about K (Table 3). There was no clear relationship between surplus production and biomass, but P_y was lowest at the highest and lowest B_y levels and autocorrelation in production process errors was obvious (Fig. 3A). The distribution of r_y values (Fig. 3B) was skewed to the right and there were no negative values. Gamma distributions fitted by maximum likelihood and the method of moments (Appendix 1) were similar in shape (Fig. 3).

Table 3

Summary statistics and gamma distribution parameters for annual process errors in the intrinsic population growth rate (r_y) for cowcod rockfish (*Sebastes levis*), estimated from stock assessment results (Butler et al.[6]). Parameters α and β, were estimated with fixed $\gamma=-M$ by maximum likelihood. K is the carrying capacity in the logistic population dynamics model. According to Butler et al.,[6] K=3400 metric tons (t) (95% confidence interval 2800–4000 t).

Parameter	K=84,500 t	K=99,400 t	K=103,000 t
Number B_y values ≤95% K	31	47	47
Sample mean	0.037	0.039	0.027
Sample variance	0.00059	0.00050	0.00021
Autocorrelation ρ	0.83	0.94	0.89
α	–0.055	–0.055	–0.055
β	17.7	19.0	36.1
$\gamma=-M$	0.0052	0.0049	0.0023
Mean	0.037	0.039	0.027
Variance	0.00048	0.00047	0.00019
Mode	0.032	0.034	0.025

With K=3400 t (Table 3), $\bar{r}$= 0.039 which suggests F_{MSY}= 0.0185/yr. This crude estimate is less than implied by the simple calculation $r = 2F_{MSY} = 0.11$ based on the proxy $F_{MSY} = M = 0.055$/yr, possibly because the natural mortality rate overestimates F_{MSY} for cowcod (Deriso, 1982). ASPIC estimates were similar (F_{MSY}=0.018/yr with an 80% bootstrap confidence interval 0.00082–0.039/yr) to estimates based on $\bar{r}_y$. In simulations for cowcod, we used $\hat{F}_{MSY}$=0.018 (from ASPIC), $\sigma^2_{r_y}$=0.00050 and ρ=0.9.

Simulation model runs indicated that cowcod are very unlikely to rebuild to B_{MSY} in ten years. The mean generation time for cowcod is about 35 years (calculated as described by Restrepo et al., 1998). Simulations indicate that the mean time for rebuilding the stock with zero F is approximately 40 years (30–50 years, depending on model type). In accord with National Standard 1 Guidelines, it may be reasonable to develop plans with the goal of rebuilding the cowcod stock in 75 years or less. We therefore calculated and plotted 75-year, rather than 10-year rebuilding time isopleths, for cowcod rockfish.

Sensitivity analyses

We conducted three sensitivity analyses for each stock to determine if the choice of statistical distribution for stochastic $r_{s,y}$ values influenced rebuilding times in simulations. Sensitivity analyses used uncorrelated process errors and no uncertainty in F_{MSY} (model type 3). The first sensitivity analysis run for each stock was a nonparametric bootstrap (Efron, 1982) with $r_{s,y}$ values drawn randomly with replacement from the observed values (Eq. 6). The second and third sensitivity analyses run for each stock were parametric bootstraps with $r_{s,y}$ values drawn from a normal or lognormal distribution with the same mean (μ) and variance (σ^2) as the observed values (Tables 2–3, Figs. 2–3). To avoid bias in runs with the lognormal distribution (Beauchamp and Olson, 1973), log-transformed $r_{s,y}$ values were drawn from a normal distribution with mean $\ln(\mu)-\tau^2/2$ and variance $\tau^2=\ln(CV^2+1)$, with CV= σ/μ (Jacobson et al., 1994). For convenience in programming, $r_{s,y}$ values in normal and lognormal runs were sampled with replacement from a fixed pool of 200 random numbers drawn from the proper statistical distribution at the outset of the simulation.

Results

Mean rebuilding times were longer than median rebuilding times in stochastic simulations (run types 2–6) for yellowtail flounder and cowcod rockfish because distributions of recovery times were skewed to the right (Figs. 4–5). Skewness (and the extent to which mean recovery times exceeded median recovery times) was more pronounced at lower starting biomass levels, at higher F levels, where there was more uncertainty about F_{MSY} and autocorrelation in process errors.

Skewed distributions for rebuilding times affected the shape of rebuilding time isopleths (Figs. 6–7). For all stochastic models of yellowtail flounder and most stochastic models of cowcod rockfish, isopleths for mean and median rebuilding times were widely separated. In addition, isopleths were asymmetrical. For example, the distance between median and $Q_{90\%}$ isopleths was greater than the distance between $Q_{10\%}$ and median isopleths. Separation of isopleths and asymmetry were greatest for model type 6 which had correlated process errors and uncertainty about F_{MSY}.

In simulations for both stocks, uncertainty about F_{MSY} had a greater effect than process error on the shape and separation between isopleths for $Q_{10\%}$, median, mean, and $Q_{90\%}$ rebuilding times. For example, in both stocks, there

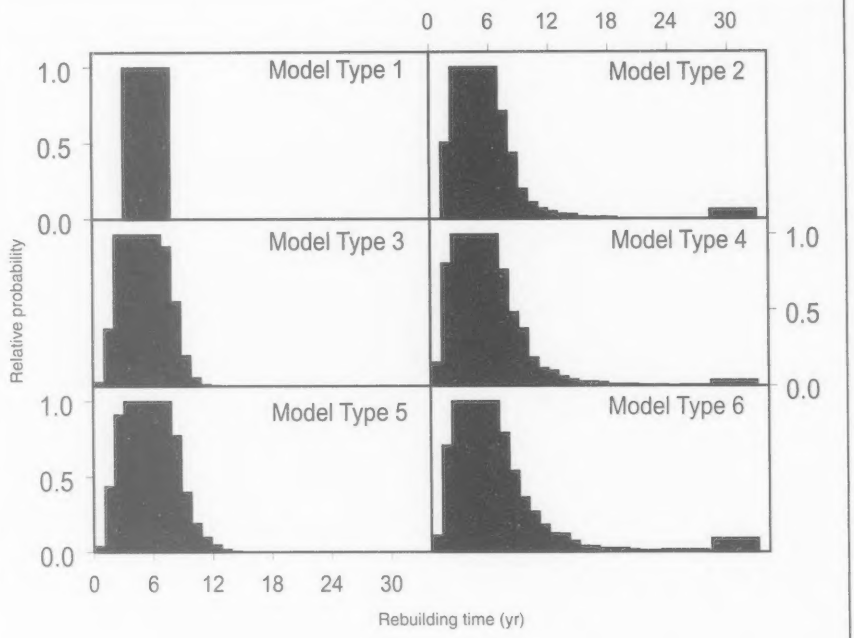

Figure 4

Distribution of simulated recovery times for Georges Bank yellowtail flounder from six types of logistic population growth models (type 1 deterministic, others stochastic, see Table 1) with F_{MSY}=0.30/yr, CV for uncertainty in F_{MSY}= zero or 20%, variance for production process errors zero or 0.037, and autocorrelation in process errors ρ=zero or 0.33. Results are for 2000 model runs starting from an initial biomass of B/B_{MSY} =0.19 and constant F=0.18/yr.

was more asymmetry and separation between isopleths (Figs. 6–7) for model type 2 (no process errors and with uncertainty about F_{MSY}) than for model type 3 (uncorrelated process error with no uncertainty about F_{MSY}).

The fishing mortality rate that gave a median recovery time of ten years for yellowtail flounder (or 75 years for cowcod rockfish) was generally higher than the fishing mortality rate that gave a corresponding mean recovery time from the same initial biomass level (Figs. 8–9). Similarly, the F that gave a mean recovery time of ten or 75 years was generally higher than the F that gave the corresponding $Q_{90\%}$ recovery time. There were some exceptions for cowcod at high F and initial biomass levels in runs with uncertainty in F_{MSY} (run types 2, 4, and 6) due to a few runs with very long rebuilding times. The very long rebuilding times in runs for cowcod with uncertainty were due to F in excess of the simulated true F_{MSY}.

Isopleth shape may be important in interpreting simulation results. For example, isopleths for 10-year median rebuilding times in all models for yellowtail flounder were steep for F in the range 0–0.2/yr (Figs. 8–9). Therefore, according to example model results, the probability of recovery in ten years is at least 50% for Georges Bank yellowtail flounder at biomass values ≥0.05 K, as long as fishing morality rates are less than 0.2/yr.

Seventy-five year stock-rebuilding time isopleths for cowcod rockfish were sensitive to assumptions about the distribution of production process errors but 10-year isopleths for yellowtail flounder were not (Figs. 10–11). We hypothesize that differences among statistical distributions r_y assumed in simulations were magnified for cowcod by long (e.g. 75 yr) rebuilding times (see "Discussion" section).

Rebuilding isopleths for cowcod based on r_y values from a gamma distribution had higher F, at a given biomass, than rebuilding isopleths based on the distribution of observed r_y values (Fig. 11). In other words, results based on the gamma distribution suggest a more productive cowcod stock, presumably because the distribution of r_y values for cowcod had more mass than the gamma distribution over low r_y values (<0.03/yr, Fig. 3).

Discussion

Managers should consider using median rebuilding time goals, in addition to mean or other quantiles, in develop-

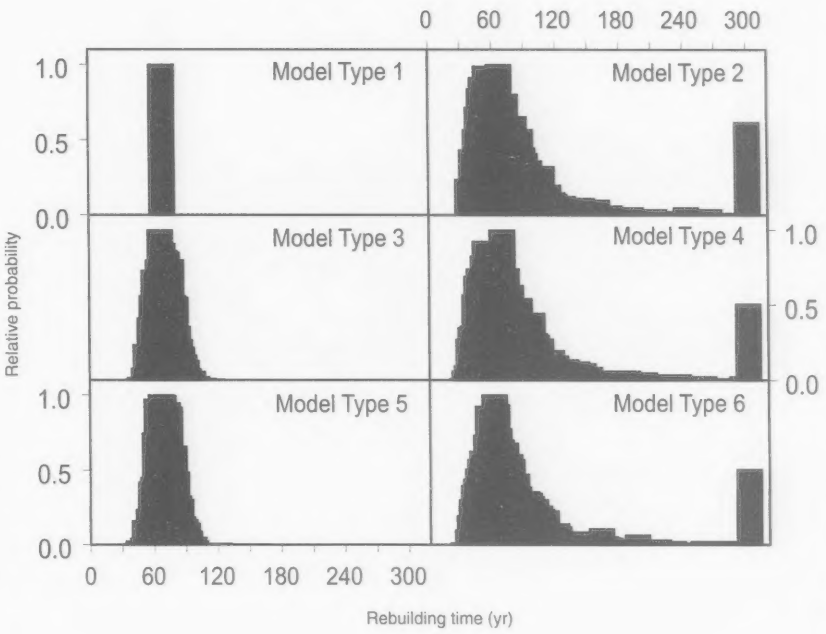

Figure 5

Distribution of simulated recovery times for cowcod rockfish in the Southern California Bight from six types of logistic population growth models (type-1 deterministic, others stochastic, see Table 1) with F_{MSY}=0.0.018 /yr, CV for uncertainty in F_{MSY}= zero or 20%, variance for production process errors zero or 0.037, and autocorrelation in process errors ρ=zero or 0.9. Results are for 2000 model runs starting from an initial biomass of B/B_{MSY} =0.19 and constant F=0.011/yr.

ing and evaluating rebuilding plans. This recommendation is based on a narrow technical consideration, i.e. that median recovery time calculations are less sensitive to model assumptions. A median rebuilding time plan is risk neutral in the sense that the probability of rebuilding times less than intended is the same as the probability of rebuilding times longer than intended (i.e. both 50%). Of course, rebuilding plans based on median rebuilding time goals will be more liberal in terms of short-term catch (i.e. have higher F) and have longer rebuilding times on average than plans based on mean or, for example, $Q_{90\%}$ rebuilding time goals. In summary, a manager who is willing to accept a 50% chance of rebuilding times greater that desired and who is concerned about model uncertainties, might choose a median rebuilding time approach.

A potential advantage in using percentiles other than the median is that managers can specify risk levels in trying to rebuild stocks. For example, managers could choose and evaluate rebuilding plans based on a $Q_{90\%}$ isopleth to insure at least a 90% chance of rebuilding in specified time period. However, $Q_{90\%}$ isopleths may be sensitive to model assumptions.

Approaches to using rebuilding time isopleths without relying on uncertain estimates of rebuilding time distributions (e.g. mean or $Q_{90\%}$), are an important area for future research. Cadrin (1999) used deterministic rebuilding time isopleths with the tenth percentile of the estimate for r. Isopleths for median rebuilding time might be used with lower bounds on confidence intervals for B_0 and B_0/K or upper bounds on current F, F_{MSY}, or F/F_{MSY}. Estimates of uncertainty in these parameters are often available (Prager, 1994) and can be incorporated in an *ad hoc* fashion. For example Butler et al.[6] suggest that B_{1998}/K for cowcod rockfish is 7% (CV about 30%) and that the F in 1998 was 0.085/yr (CV 34%). A risk-averse manager might implement a rebuilding plan that reduces that $F_{Threshold}$ to a point on the 75-year rebuilding time isopleth that lies above the lower boundary of a 95% confidence interval for biomass. Similarly, a risk-averse manager might select a rebuilding plan that reduces $F_{Threshold}$ to account for the upper bound on uncertainty in estimating F.

Uncertainty in F_{MSY} is an important factor to consider in rebuilding plans as F increases from low levels towards F_{MSY}. Expected rebuilding times increase at high F because F may exceed true F_{MSY} (assumed known but with

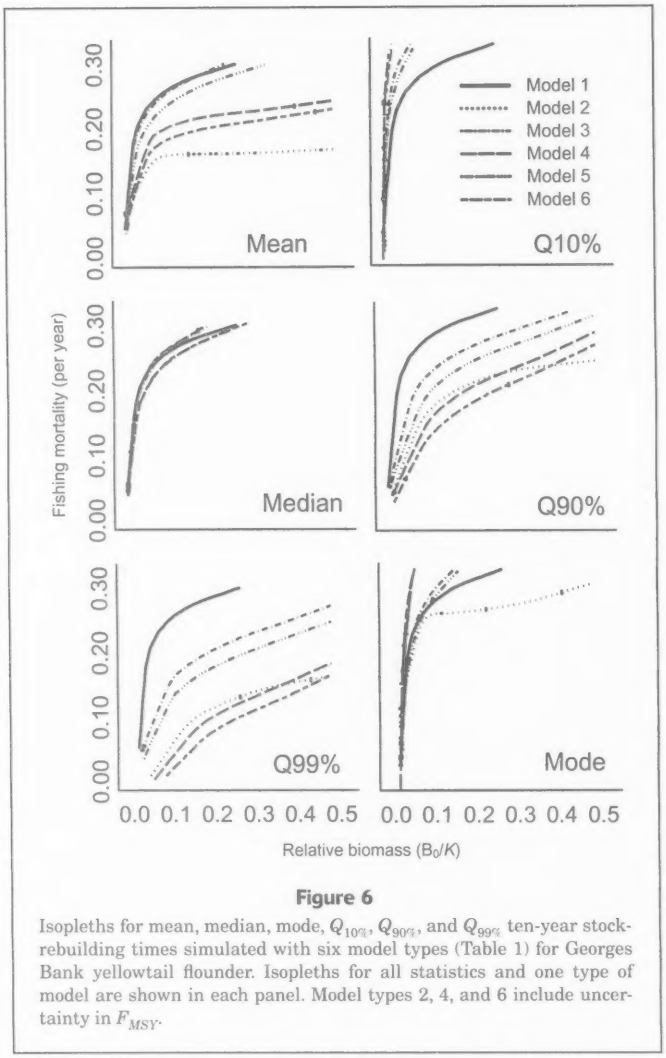

Figure 6

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ ten-year stock-rebuilding times simulated with six model types (Table 1) for Georges Bank yellowtail flounder. Isopleths for all statistics and one type of model are shown in each panel. Model types 2, 4, and 6 include uncertainty in F_{MSY}.

error) in a high proportion of cases (Figs. 8–9). Fortunately, process errors and autocorrelation may reduce this problem because stock growth rates increase in some years so that the true F_{MSY} exceeds the manager's estimate.

Stock-rebuilding times calculated with deterministic models approximate median rebuilding times from stochastic models. For example, rebuilding times in Cadrin (1999) calculated with a deterministic model for Georges Bank yellowtail flounder are very close to median rebuilding times from our stochastic models. From our results, we hypothesize that rebuilding time isopleths for other species (Applegate et al.[3]) based on Cadrin's (1999) deterministic model should also be viewed as approximations to isopleths for median rebuilding times.

Our simulation analyses indicate that rebuilding times for overfished stocks (with a range of life history characteristics, initial biomass levels and fishing mortality rates) tend to be skewed and can be highly variable (Figs. 4–5). Hence, rebuilding in any specific case may be quicker or take much longer than expected, particularly if expectations are based on deterministic models that approximate median rebuilding times. For example, probabilities of rebuilding times twice as long as the goal for Georges Bank yellowtail flounder (10 yr) and cowcod (75 yr) were 4% and 8% and probabilities of rebuilding times half as long were 40% and 1%.

Modeling choices

Stochastic models are necessary when estimates of mean rebuilding times or quantiles other than the deterministic approximation to the median are needed. Rebuilding time

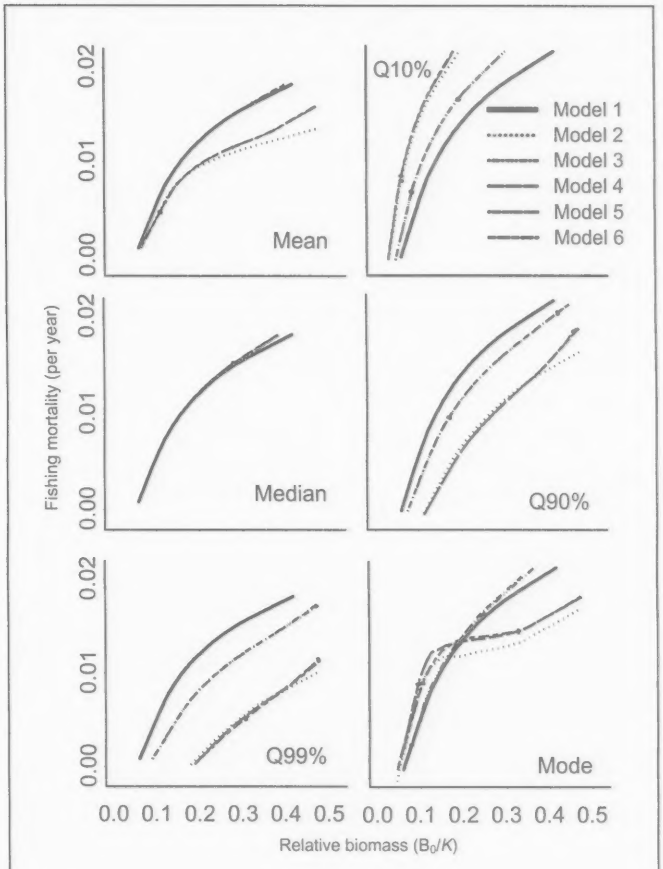

Figure 7

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ 75-year stock-rebuilding times simulated with six model types (Table 1) for cowcod rockfish in the Southern California Bight. Isopleths for all statistics and one type of model are shown in each panel. Model types 2, 4, and 6 include uncertainty in F_{MSY}.

isopleths from deterministic model type 1 were quite different from isopleths (other than for median rebuilding times) from stochastic models.

Rebuilding time isopleths can be used with any type of population dynamics model. We used the logistic population growth model in this paper because it is clearly linked to B_{MSY} and F_{MSY}, incorporates density dependence, is easy to apply to a wide range of stocks (with varying amounts of information), and computationally efficient. However, rebuilding time isopleths could have been calculated by using Cadrin's[5] age-structured model for Georges Bank yellowtail flounder or Butler et al.'s[6] biomass dynamic model for cowcod rockfish. Age-structured models might be best for calculating rebuilding time isopleths if the rebuilding time frame is relatively short and estimates of abundance are available for several incoming year classes because age-structured models account for transient conditions (e.g. recruitment and growth patterns) that are important in the short term.

Age-based projections were used to test the expected performance of rebuilding targets for six New England groundfish stocks (NDWG[8]). The original rebuilding targets were derived from five-year rebuilding time isopleths calculated with a deterministic logistic growth models, but the targets incorporated estimation uncertainty by assuming the tenth percentile of the estimate

[8] NDWG (Northern Demersal Working Group). 2000. Assessment of 11 northeast groundfish stocks through 1999. Northeast Fisheries Science Center Reference Document 00-05, 175 p. Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA, 02543.

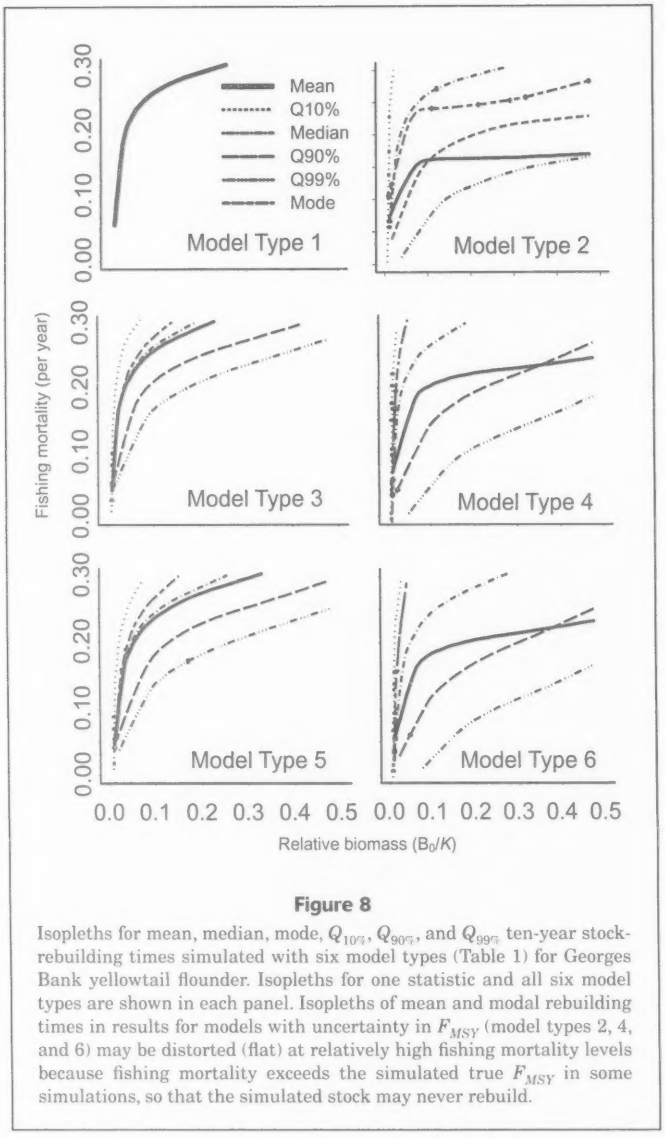

Figure 8

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ ten-year stock-rebuilding times simulated with six model types (Table 1) for Georges Bank yellowtail flounder. Isopleths for one statistic and all six model types are shown in each panel. Isopleths of mean and modal rebuilding times in results for models with uncertainty in F_{MSY} (model types 2, 4, and 6) may be distorted (flat) at relatively high fishing mortality levels because fishing mortality exceeds the simulated true F_{MSY} in some simulations, so that the simulated stock may never rebuild.

of r (Cadrin, 1999; Applegate et al.[3]). For the six stocks, starting biomass in 1999 ranged from 25% to 93% of B_{MSY} and estimates of F_{MSY} ranged from 0.5 to 0.8. Estimated rebuilding times averaged 3.5 years (ranging from 1 to 7 yr) for 50% probability of attaining B_{MSY} (NDWG[8]). Therefore, the age-based simulations indicated that isopleths based on deterministic biomass dynamic models generally performed well for overfished New England groundfish stocks. Brodziak et al. (2001) analyzed stock-recruit data and concluded that "(1) time horizons for rebuilding will be uncertain, owing to recruitment variability, (2) some productive stocks (haddock, yellowtail flounder) have serial correlation in recruitment and this may either enhance or diminish chances for stock recovery." Thus, results with surplus production models, age-structured models, and stock-recruit analyses highlight the fundamental similarities between a wide range of modeling approaches (Sissenwine and Shepherd, 1987).

The best choice of stochastic simulation model for developing and evaluating rebuilding plans will depend on the situation. Sainsbury (1993) concluded that models incorporating simple assumptions about population dynamics were more appropriate for evaluating performance of control rules than models with more complex assumptions. PFMC[1] used a simple model incorporating environmental effects on recruitment with useful results. However, Bell

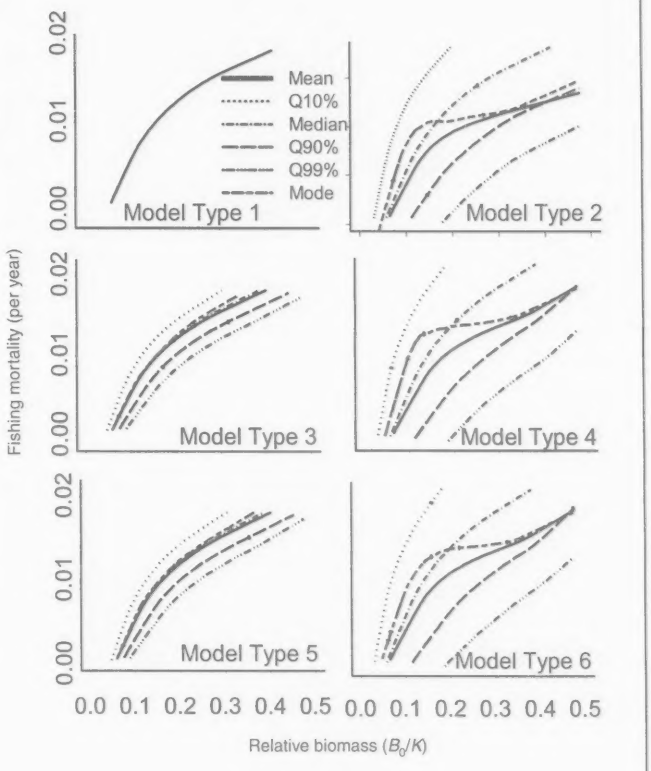

Figure 9

Isopleths for mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ 75-year stock-rebuilding times simulated with six model types (Table 1) for cowcod rockfish in the Southern California Bight. Isopleths for one statistic and all six model types are shown in each panel. Model types 2, 4, and 6 include uncertainty in F_{MSY}. Isopleths of mean and modal rebuilding times in results for models with uncertainty in F_{MSY} (model types 2, 4, and 6) may be distorted (flat) at relatively high fishing mortality levels because fishing mortality exceeds the simulated true F_{MSY} in some simulations so that the simulated stock may never rebuild.

and Stefansson[9] and Patterson (1999) used more complex simulation models with success.

Distributional assumptions

Simulation analyses (Figs. 10–11) indicate that the choice of statistical distribution for simulating process errors in model parameters (e.g. r_y) may be important, particularly when rebuilding times are long (e.g. those for cowcod rockfish) due to low stock productivity, low stock biomass, unproductive stock dynamics, or autocorrelation in process errors. The choice of statistical distributions for simulating r_y involves choosing between theoretical distributions supported by theory (e.g. autocorrelated gamma distribution with negative values bounded below at $-M$) or bootstrap distributions of observed values. The programming and work required to experiment with alternative distributions is not overwhelming and we recommend sensitivity analyses in cases where distributional assumptions may be important.

Theoretical distributions for stochastic parameters are flexible because many types of distributions are available, most can be modified to include autocorrelation, most can

[9] Bell, E. D., and G. Stefansson. 1998. Performance of some harvest control rules. NAFO (North Atlantic Fisheries Organization) SCR Doc. 98/7, 1–19. Northwest Atlantic Fisheries Organization, 2 Morris Drive, P. O. Box 638, Dartmouth, Nova Scotia, B2Y 3Y9, Canada.

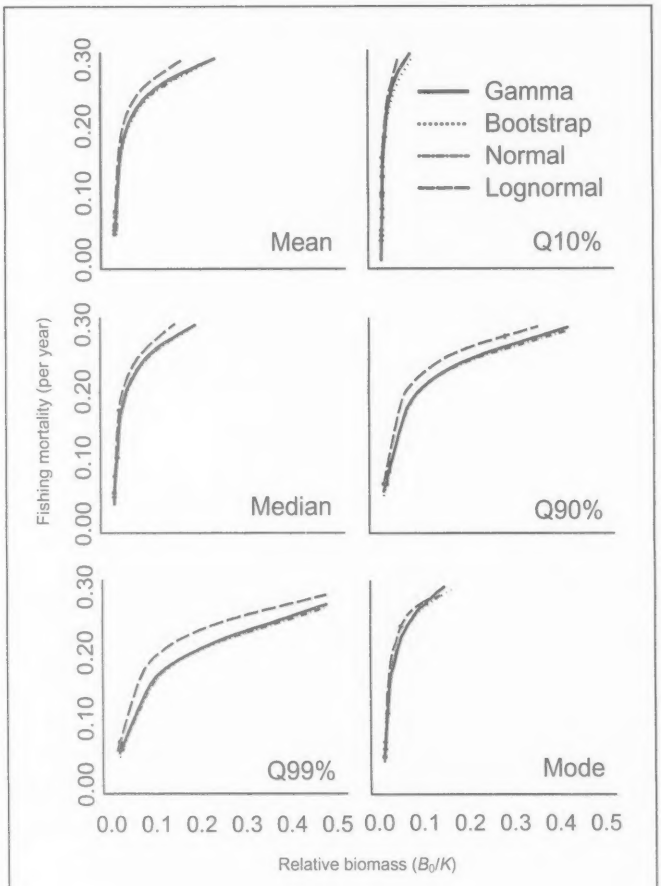

Figure 10

Mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ ten year stock-rebuilding time isopleths for Georges Bank yellowtail flounder, simulated with model type 3 (no uncertainty about F_{MSY} and uncorrelated r_y values). Stochastic r_y values were from a gamma distribution (same as Figs. 6 and 8), normal distribution, lognormal distribution, or bootstrap of observed r_y values. All distributions had the same mean and variance.

be modified to include negative or extreme values not evident in short observed time series, and most can give the same mean, variance and autocorrelation levels as estimated from available data. However, as in the case of Georges Bank yellowtail flounder and cowcod, the shape of theoretical and observed distributions may not match closely (Figs. 2–3).

In comparing theoretical and observed distributions for model parameters (e.g. Figs. 2–3), it is important to remember that most observed distributions are based on relatively few observations (Table 2). Furthermore, observed values may be autocorrelated (ρ=0.33 for Georges Bank yellowtail flounder and ρ=0.94 for cowcod rockfish, Tables 2–3). High levels of autocorrelation reduce the "effective" number of observations dramatically so that observed values may provide a poor estimate of the shape of their distribution (Bartlett, 1946; Bayley and Hammersley, 1946). For example, Equation 16 in Bayley and Hammersley, with estimated autocorrelations (lags of 1–13 years) for Georges Bank yellowtail flounder, gives an effective sample size n^*=17 (compared to n=25 r_y values). For cowcod rockfish (with autocorrelations for lags 1–17), n^*=11 (compared to n=47 r_y values). Thus, autocorrelation in r_y values may reduce the effective sample size and information used to estimated the shape, mean and variance of statistical distributions for r_y values by about 32% for Georges Bank yellowtail flounder and 77% for cowcod rockfish.

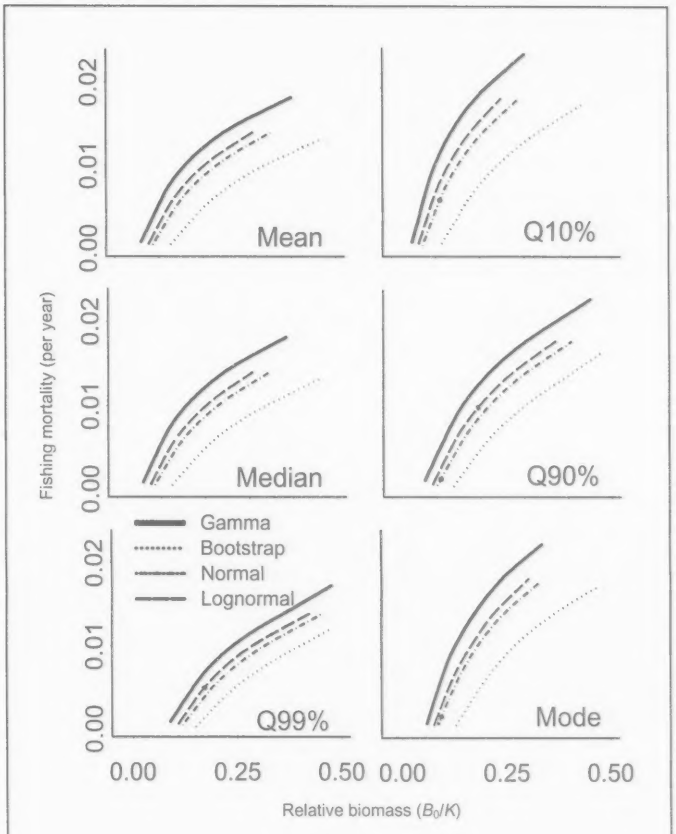

Figure 11

Mean, median, mode, $Q_{10\%}$, $Q_{90\%}$, and $Q_{99\%}$ 75-year stock-rebuilding time isopleths for cowcod rockfish, simulated with model type 3 (no uncertainty about F_{MSY} and uncorrelated r_y values). Stochastic r_y values were from a gamma distribution (same as Figs. 7 and 9), normal distribution, lognormal distribution or bootstrap of observed r_y values. All distributions had the same mean and variance.

Developing, monitoring, and evaluating stock-rebuilding programs

Once the management goal, desired probability of achieving the stock-rebuilding goal, and the time frame for rebuilding are identified (e.g.10-yr median rebuilding time to a B_{MSY} target), the simplest way to use stock-rebuilding time isopleths in designing a rebuilding plan is to choose a constant-$\bar{F}_{B_0}$ level from the appropriate rebuilding time isopleth, based on a current estimate of B_0. Cadrin (1999) has provided an example of this approach.

Stock-rebuilding time isopleths can be used to monitor the progress of any rebuilding plan although interpretation is clearest with constant-F values (Cadrin, 1999). For example, the point defined by current biomass and F for Georges Bank yellowtail flounder in the second year (1997) of a hypothetical five-year rebuilding plan beginning in 1996 should lie near or within the 3-year rebuilding time isopleth (Fig. 1). If the point lies far outside the 3-year isopleth, then managers could be sure that the rebuilding plan was behind schedule.

Evaluating harvest control rules as stock-rebuilding programs

It may be necessary to evaluate harvest control rules that allow F to vary with biomass (e.g. the common harvest control rule in Fig. 1) as a rebuilding plan. Rebuilding isopleths provide guidance in this situation because they can be used to reject some harvest control rules based on a single necessary criterion. However, the test is weak because a harvest control rule that passes the test may or

may not be sufficient as a rebuilding plan. In this context, it is important to remember that rebuilding time isopleths are constructed based on the assumption of constant fishing mortality rates during the rebuilding program. More complicated rebuilding plans, that allow F to vary according to changes in biomass or other factors, are best evaluated by stock-specific simulations.

The test is based on the notion that control rules that allow F levels above the stock-rebuilding time isopleth for biomass levels above B_0 are unlikely to rebuild the stock with desired probability in the desired time frame. Therefore, as a minimum requirement for meeting rebuilding time goals, harvest control rules used as rebuilding plans should lie on or under the corresponding rebuilding time isopleth for all biomass levels above B_0. Consider a hypothetical overfished stock for which there is a ten-year median rebuilding time goal. Assume that a harvest control rule proposed as a rebuilding plan has the typical shape (i.e. F increases or stays the same as biomass increases, as in Fig. 1). If the control rule lies above the isopleth for some critical biomass level between B_0 and B_{MSY}, then the rule will allow fishing mortality rates that are generally too high to meet management goals once biomass reaches the critical level.

The example of Georges Bank yellowtail flounder

Georges Bank yellowtail flounder (Fig. 1) can be used to illustrate how rebuilding time isopleths might have been used to evaluate stock-rebuilding plans for hypothetical implementation during 1996 and how stock-rebuilding time isopleths can be used to monitor progress in rebuilding overfished stocks. The discussion is hypothetical, however, because the examples evaluate management approaches that have not been used in rebuilding the stock. In reality, managers kept F for Georges Bank yellowtail flounder during 1996–99 nearly constant at a level well the below the 10-year isopleth, and the Georges Bank yellowtail flounder stock was almost rebuilt to the B_{MSY} target level in 1999 after only four years (Fig. 1).

Based on this example, the harvest control rule in Figure 1 would have been marginal for use in a hypothetical median ten-year stock-rebuilding plan for Georges Bank yellowtail flounder starting in 1996, because the rule lies slightly above the 10-year isopleth for biomass levels of 47% B_{MSY}. The harvest rule might have been rejected outright as a five-year rebuilding plan because the rule lies well above the 5-year rebuilding time isopleth. The rebuilding trajectory for Georges Bank yellowtail flounder (Fig. 1) shows that the five-year rebuilding plan, which began in 1996, was on schedule during 1996–98 because fishing mortality and estimated biomass were within the 5-year, 4-year, and 3-year isopleths during successive years.

The Georges Bank yellowtail flounder example provides an important final lesson about uncertainty in actual rebuilding times, even if statistical distributions of potential rebuilding times are characterized accurately. During 1996–99, the stock was managed at a relatively constant F level that was well above the entire 4-year median rebuilding time isopleth (Fig. 1). Despite the relatively high F level, Georges Bank yellowtail flounder reached a biomass level near B_{MSY} in 1999, after four years. We attribute this fortunate chain of events to stochastic variation in process errors stemming primarily from recruitment and growth of the strong 1997 year class (Cadrin[5]).

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Appendix 1—Independent process errors

We simulated independent production process errors using a three-parameter gamma probability distribution (Johnson et al., 1994). The gamma probability density function for independent (no autocorrelation) r_y values in one simulation (denoted as s) was

$$P(r_{s,y} \mid \alpha_s, \beta_s, \gamma) = \frac{(r_{s,y} - \gamma)^{\alpha_s - 1} e^{-(r_{s,y} - \gamma)/\beta_s}}{\beta_s^{\alpha_s} \Gamma(\alpha_s)}, \quad (1)$$

where $\Gamma(\alpha_s)$ is the gamma function and the parameters of the gamma distribution are $\alpha_s > 0$, $\beta_s > 0$ and γ.

The expected (mean) value for r_y values from the three-parameter gamma distribution is $\beta_s \alpha_s + \gamma$ and the variance is $\beta_s^2 \alpha_s$. The parameter γ defines a minimum value for the distribution of r_y values; therefore we set $\gamma = -M$ (see text). There were too little data to directly estimate the lower-bound γ for either of the species in our analysis because years with negative production occurred infrequently for stocks in our analysis. The three-parameter gamma distribution has a single mode at $\gamma + \beta_s(\alpha_s - 1)$ if $\alpha_s > 1$. When $\alpha_s \leq 1$, the probability distribution function declines monotonically as r_y increses from the minimum value at $r_y = \gamma$.

The mode for empirical r_y values in our study was always larger than $-M$ so that α_s was larger than one.

Maximum likelihood estimates of the parameters α and β for each stock (conditional on the assumption $\gamma=-M$) were obtained iteratively in a spreadsheet by maximum likelihood with observed r_y values as data. In simulations, we used the simpler method of moments to calculate gamma distribution parameters. Given $\gamma=-M$ and estimates of the mean (μ) and variance (σ^2) for r_y values from real data, the method of moments solves the two equations $\mu=(B\alpha+\gamma)$ and $\sigma^2=\alpha\beta^2$ for the two unknowns α and β. In particular $\beta=\sigma^2/(\mu-\gamma)$ and $\alpha=\sigma^2/\beta^2$. The maximum likelihood approach and method of moments gave similar parameter estimates for real data sets (Figs. 2–3) suggesting that the method of moments was acceptable for simulations. In what comes later, maximum likelihood parameter estimates from data ($\hat{\alpha}$, $\hat{\beta}$, $\gamma=-M$) are distinguished from simulated values calculated by the method of moments ($\tilde{\alpha}_s$, $\tilde{\beta}_s$, $\gamma=-M$).

In each simulation run, the assumed "true" value of $F_{MSY,s}$ was used to calculate $\bar{r}_s = 2F_{MSY,s}$. In simulation runs with no process error the simple calculation $r_{s,y}=\bar{r}_s$ was used. In runs with process error, $\bar{r}_s$, was the mean of the distribution of stochastic $r_{s,y}$ values (see below).

For runs with independent process errors (no autocorrelation), annual logistic parameter values $r_{s,y}$ were drawn from a gamma distribution with parameters ($\tilde{\alpha}$, $\tilde{\beta}$, γ) calculated by the method of moments from the mean $\bar{r}_s$ and variance $\sigma^2_{r_y}$ estimated from empirical data.

Appendix 2—Autocorrelated process errors

This appendix describes two algorithms for generating autocorrelated production process errors from gamma distributions. The algorithms are based on first-order autoregressive and moving average error structures used in time-series analysis (Nelson, 1973). The shapes of original uncorrelated gamma distributions and new, correlated probability distributions for both algorithms appeared identical in plots.

Algorithm 1 was for autocorrelations (ρ) in the range zero to 0.5:

$$r_{s,y} = d_{s,y} + \theta d_{s,y-1}, \tag{1}$$

where $r_{s,y}$ = was the logistic population growth parameter for year y in simulation run s, and the moving average parameter (θ) was

$$\theta = -1+\frac{\sqrt{1-4\rho^2}}{2\rho}, \tag{2}$$

with θ in the range (0,1). The random numbers $d_{s,y}$ in algorithm 1 were drawn from a gamma distribution with parameters:

$$\ddot{\alpha}_s = \tilde{\alpha}_s \frac{(1+\theta^2)}{(1+\theta)^2} \tag{3}$$

$$\tilde{\beta}_s = \tilde{\beta}_s \frac{(1+\theta)}{(1+\theta^2)} \tag{4}$$

and $\gamma=-M$. The adjusted parameter values ($\ddot{\alpha}_s$, $\ddot{\beta}_s$, γ) make the mean and variance of autocorrelated $r_{s,y}$ values from algorithm 1 the same as for an independent series drawn from a gamma distribution with parameters $\tilde{\alpha}_s, \tilde{\beta}_s, \gamma$ (see Appendix 1).

Algorithm 2 was for autocorrelations (ρ) in the range (0.5, 1):

$$r_{s,y} = \frac{\sum_{j=1}^{L} d_{s,y-1-j}}{L}, \tag{5}$$

where the random numbers $d_{s,y}$ were drawn from gamma distributions with parameters $\ddot{\alpha}_{s,r} = \tilde{\alpha}_{s,r}/L$, L an integer >3, $\ddot{\beta}_{s,r} = \beta_{s,r}L$, and γ. The adjusted parameter values make the mean and variance of the autocorrelated and independent $r_{s,y}$ values the same.

The autocorrelation in algorithm 2 is $\rho=(L-1)/L$. For simulations, we chose the smallest value of L that gave an autocorrelation that was at least as large as the value desired. Extremely high autocorrelations (e.g. $\rho>0.9$) can give $\ddot{\alpha}_{s,y} = \tilde{\alpha}_{s,y}/L \leq 1$ when $\tilde{\alpha}_{s,r}$ is near L. This was a minor problem in some cases because gamma distributions for $d_{s,y}$, and autocorrelated values of $r_{s,y}$, have no mode when $\ddot{\alpha}_{s,y} \leq 1$. We avoided this, where necessary, by setting the maximum value of L to 10 (ρ=0.90) and constraining $\ddot{\alpha}_{s,y} \leq 1$ in simulations.

Nuclear and mitochondrial DNA markers for specific identification of istiophorid and xiphiid billfishes*

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Abstract—Independent molecular markers based on mitochondrial and nuclear DNA were developed to provide positive identification of istiophorid and xiphiid billfishes (marlins, spearfishes, sailfish, and swordfish). Both classes of markers were based on amplification of short segments (<1.7 kb) of DNA by the polymerase chain reaction and subsequent digestion with informative restriction endonucleases. Candidate markers were evaluated for their ability to discriminate among the different species and the level of intraspecific variation they exhibited. The selected markers require no more than two restriction digestions to allow unambiguous identification, although it was not possible to distinguish between white marlin and striped marlin with any of the genetic characters screened in our study. Individuals collected from throughout each species' range were surveyed with the selected markers demonstrating low levels of intraspecific character variation within species. The resulting keys provide two independent means for the forensic identification of fillets and for specific identification of early life history stages.

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Species-level identification of most marine fishes is typically based on adult characters. However, distinguishing characters may be removed from adults when they are processed for market or personal consumption, making such identification problematic. Furthermore, species identification from early life history stages of many marine fishes is not possible because diagnostic morphological characters at these stages are not currently known. Consequently, alternative means of identification are needed.

A variety of molecular genetic characters have been used to provide identifications of marine fishes. Marine fish eggs and larvae have been identified by using allozymes (Mork, et al., 1983; Graves et al., 1988), restriction analysis of whole mitochondrial (mt) DNA (Daniel and Graves, 1994), restriction analysis of specific mtDNA gene regions (Luczkovich et al.[1]), and specific amplification of mtDNA gene regions (Rocha-Olivares, 1998). A similar suite of molecular markers has been used to provide positive identification of adult marine fish tissues, with recent emphasis on restriction analysis of amplified regions of the mitochondrial genome (Chow et al., 1993; Chow 1994, Chow and Kishino, 1995; Heist and Gold, 1997; Innes et al., 1998; Cordes et al., 2001).

To be effective, a diagnostic molecular marker must demonstrate consistent differences among closely related species and exhibit very limited intraspecific variation. Restriction analyses of regions of the mitochondrial genome have met these criteria for several marine fishes. However, reliance on a single, maternally inherited character (mtDNA) can provide misleading results in situations where there is a possibility of hybridization or introgression, and analyses of both nuclear and mitochondrial markers are therefore desirable.

The istiophorid and xiphiid billfishes (marlins, spearfishes, sailfish and swordfish) represent an important commercial and recreational fisheries resource. Because of depleted stock levels, current regulations within the United States prohibit the sale of istiophorid billfish taken in the Atlantic Ocean. Although adult billfishes are easily identified on the basis of morphological characters, these characters are typically removed during processing, preventing morphological identification. In addition, the early life history stages of istiophorid billfishes are not well known, and specific identification is problematic (Nakamura, 1985).

Chow (1994) used 13 restriction enzymes in a restriction fragment length polymorphism (RFLP) analysis of a 350-bp region of the mtDNA cytochrome *b* gene to discriminate among ten nominal species of billfishes; however samples sizes were small for several species

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[1] Luczkovich, J. J., H. J. Daniel, M. W. Sprague, S. E. Johnson, R. C. Pullinger, T. Jenkins, and M. Hutchinson. 1999. Characterization of critical spawning habitats of weakfish, spotted seatrout and red drum in Pamlico Sound using hydrophone surveys. Final report to the North Carolina Division of Marine Fisheries under grant numbers F-62-1 and F-62-2, 128 p. North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries. Morehead City, NC 28557.

and banding patterns differed by as little as 15 base pairs, making alternate patterns difficult to distinguish. Innes et al. (1998) were able to discriminate among seven species of billfish found in Australian waters with RFLP analysis of a 1400-bp region of the mtDNA control region (D-loop). Their analysis, which employed four restriction enzymes, revealed relatively high levels of intraspecific variation of the diagnostic characters within some species, and there was some overlap of banding patterns between species. In neither study was an independent nuclear marker developed to corroborate specific identifications based on analyses of mtDNA.

In this article we present a molecular key to the identification of istiophorid and xiphiid billfishes using RFLP analyses of independent mitochondrial and nuclear DNA regions. We demonstrate low intraspecific variation of the characters within large collections of individuals sampled from throughout each species' range and show the utility of the markers for the identification of fillets and early life history stages.

Materials and methods

Collections of striped marlin (*Tetrapturus audax*), white marlin (*Tetrapturus albidus*), blue marlin (*Makaira nigricans*), and sailfish (*Istiophorus platypterus*) were available from previous analyses of stock structure (Graves and McDowell 1994, 1995; Graves, 1998), and individuals from locations throughout each species' range were selected for the present study (Table 1). These DNA samples consisted of the nuclear and mitochondrial bands resulting from mtDNA purifications with the equilibrium density gradient centrifugation protocols of Lansman et al. (1981). Samples of black marlin (*Makaira indica*), longbill spearfish (*Tetrapturus pfluergeri*), shortbill spearfish (*Tetrapturus angustirostris*), and swordfish (*Xiphias gladius*), were obtained from recreational and commercial fishermen (Table 1) and consisted of either frozen heart tissue or white muscle tissue preserved in DMSO storage buffer (Seutin et al., 1991). DNA was extracted from these tissues following the protocols of Winnepenninckx et al. (1993).

Evaluation of candidate mitochondrial and nuclear loci involved a two-step process. The first was to ensure consistent amplification by the polymerase chain reaction (PCR) of a similar-size product across all taxa. The second step was to screen those loci that successfully amplified across all billfish species with a panel of restriction endonucleases to identify enzymes that discriminated among species and revealed limited intraspecific variation.

Several candidate mitochondrial and nuclear gene regions were amplified by PCR (Table 2). The 25 μL PCR reactions consisted of 0.25 μL template DNA, 2.5 μL 10X PCR buffer plus magnesium, 0.5 μL dNTP mix, 0.25 μL forward primer, 0.25 μL reverse primer, 0.125 μL *Taq* DNA polymerase, and 21.125 μL PCR grade water. Primers were ordered from either Life Technologies (Gaithersburg, MD) or Genosys Biotechnologies Inc. (The Woodlands, TX), and PCR reactions were carried out in an MJ Research Corporation PTC-200 Peltier thermal cycler (Watertown, MA) by using the Life Technologies PCR reagent system (Gaithersburg, MD). Initial screening demonstrated that the mitochondrial ND4 gene region and the nuclear MN32-2 locus produced the most reliable amplifications across taxa and PCR conditions were optimized for these loci. The cycling parameters for the ND4 gene region were an initial denaturation at 95°C for 5 min., followed by 35 cycles of 94°C for 1 min., 47°C for 1 min., 65°C for 3 min., and a final extension at 65°C for 7 min. Amplification of MN32-2 proceeded with an initial denaturation at 95°C for 5 min., 40 cycles of 94°C for 1 min., 57°C for 1 min., 65°C for 3 min., and a final extension at 72°C for 7 min. Amplified products were held at 4°C until use. The size of each amplification product was determined on a 1% agarose gel run in TBE (45 mM Tris, 45 mM boric acid, I mM EDTA) at 100 volts for 1 hour. ND4 amplification resulted in a product of approximately 1.7 kb and MN32-2 amplification resulted in a product of approximately 1.2 kb.

Amplified products were screened with a panel of restriction endonucleases to identify those that discriminated among species, and revealed a minimum level of variation within species. All enzymes were purchased from Gibco/BRL Life Technologies Inc. (Bethesda, MD) with the exception of *Ban*I, which was purchased from Promega (Madison, WI). All were used according to the manufacturers' instructions.

Restriction fragments were separated on 2.5% horizontal agarose gels made from 1.25% UltraPure agarose (Life Technologies Inc., Bethesda, MD) and 1.25% NuSeive

Table 1
Collection information for billfish samples surveyed.

Species	Location	Number	Total
Sailfish	Brazil	34	99
	Mexico	24	
	Ecuador	17	
	Australia	24	
White marlin	Brazil	38	99
	Morocco	36	
	Venezuela	25	
Striped marlin	Mexico	28	96
	Ecuador	38	
	Australia	30	
Black marlin	Ecuador	12	60
	Australia	48	
Spearfish	Venezuela	12	16
	Hawaii	4	
Blue marlin	Mexico	24	150
	Australia	4	
	Ecuador	20	
	Hawaii	63	
	Jamaica	39	
Swordfish	Hawaii	20	20

Table 2

Primer pairs used to amplify regions evaluated in this study.

Locus	Primer sequence (5′–3′)	Source
Cytochrome b:		
CYTB-F	TGGGSNCARATGTCNTWYTG	Joseph Quattro, personal commun.[1]
CYTB-R	GCRAANAGRAARTACCAYTC	
ATPase 6:		
ATPase L8331	TAAGCRNYAGCCTTTTAAG	Joseph Quattro, personal commun.[1]
ATPase H8969	GGGGNCGRATRAANAGRCT	
D-Loop:		
CB3R-L	CATATTAAACCCGAATGATATTT	Palumbi et al., 1991
12SAR-H	ATAGTGGGGTATCTAATCCCAGTT	
ND4:		
ND4 ARG-BL	CAAGACCCTTGATTTCGGCTCA	Bielawski and Gold, 1996
ND4 LEU	CCAGAGTTTCAGGCTCCTAAGACCA	
ITS:		
ITS-3	TATGCTTAAATTCAGCGGGT	Goggin, C.L, 1994
ITS-5	CGTAGGTGAACCTGCGGAAGG	
SACTIN:		
SACSMSF-F	CGGACGCCCCCGTCACCAGGTAC	This study
SACIN-R	CCAGAGGCATACAGGGACAGCACAGC	
MN32-2:		
MN32-2F	GTAGCAAGGGGCTGTTGCATAG	Buonaccorsi et al., 1999
MN32-2R	GAGTCAGTGGTTCGGGATTTTATC	
MN47:		
MN47-F	GCTGTTGACCCAAACAATCCGG	Buonaccorsi et al., 1999
MN47-R	GGGCATAAATGCTCAGGACACTT	
MN81:		
MN81-F	CACTCAAACAGGTGAATCCTGGC	Buonaccorsi et al., 1999
MN81-R	CAAAACAACAGATGCCGCTAAGG	
WM08:		
WM08F	AGCAGCTAGGGACACACGATTCC	Buonaccorsi et al., 1999
WM08R	GGCAAACCTTACACTGAGGGGATG	

[1] Quattrro, J. 1995. Personal commun. Department of Biological Sciences, University of South Carolina College of Science and Mathematics, Columbia, SC, 29208.

GTG agarose (FMC BioProducts, Rockland, ME), and visualized under UV light after having been stained with ethidium bromide. Fragment sizes were estimated by comparison with a 1-kb size standard (Life Technologies Inc., Bethesda, MD) using RFLPScan Plus 3.0 (Scanalytics, Billerica, MA).

Results

Mitochondrial marker

Four mtDNA regions (cytochrome *b*, D-loop, ND4, and ATPase) were included in the initial screening (Table 2). The ATPase region was tested with eight potentially useful enzymes based on published sequences and was found to have an extremely low level of interspecific variation (many species exhibiting identical banding patterns). The cytochrome *b* region was screened with four enzymes based on published sequences, but because of the small size of the amplification product (350bp), differences in banding patterns were small and difficult to distinguish. The D-loop region was screened with a total of 40 enzymes. Of these, *Bcl* I, *Alu* I, *Rsa* I, and *Hinf* I were tested with up to 50 individuals from each species. Banding patterns that were initially thought to be diagnostic for blue marlin based on *Rsa* I were found to occur at low frequency in sailfish. This overlap combined with the large amount of intraspecific variation in some species made this region unsuitable for use as a forensic marker. Finally, the ND4 region was screened with a total of 47 restriction enzymes. Of these, 17 were tested more extensively, and the combi-

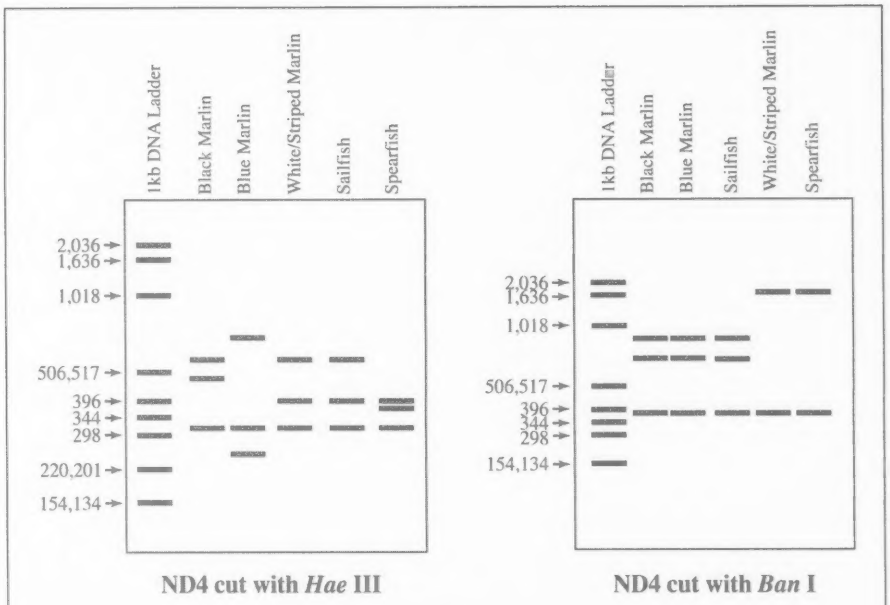

Figure 1

ND4 gel. Most common restriction fragment patterns of the ND4 mitochondrial gene region of istiophorid billfishes. (**A**) Digestion with *Hae* III. From left to right, 1-kb DNA ladder, black marlin (pattern D), blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern B), shortbill spearfish (pattern E), and longbill spearfish (pattern E). (**B**) Digestion with *Ban* I. From left to right, 1-kb DNA ladder, black marlin (pattern A), blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern A), shortbill spearfish (pattern B), and longbill spearfish (pattern B).

Table 3

Restriction fragment patterns of the mitochondrial ND4 region of istiophorid and xiphiid billfishes. Only diagnostic bands are shown.

(**A**) Digestions with *Hae* III. A = blue marlin; B = striped marlin, white marlin, sailfish; C = white marlin, sailfish; D = black marlin; E = spearfish; F = white marlin; G = spearfish; H = swordfish.

A	B	C	D	E	F	G	H
800	570	800	570	405	570	405	950
320	405	405	530	380	405	320	300
270	320	320	320	320	380	270	290

(**B**) Digestions with *Ban* I. A = blue marlin, sailfish, black marlin, spearfish; B = striped marlin, white marlin, spearfish; C = swordfish.

A	B	C
850	1500	700
650	400	650
400		400

nation of *Ban* I and *Hae* III was found to be diagnostic and to reveal a low level of intraspecific variation.

After finding diagnostic enzymes for use with the ND4 region, a total of 540 billfish samples was screened (Table 1) to evaluate the accuracy of the marker. Samples from a broad geographic range, including both the Atlantic and Indo-Pacific, were used for each species whenever possible. Of these, the white marlin, spearfishes and sailfish each exhibited one alternative restriction pattern for *Hae* III at low frequency (3.6%, 20.0% and 7.4% respectively) but in no case was the alternate pattern the same as a pattern seen in another species (Table 3). In addition, spearfishes exhibited an alternate pattern for the enzyme *Ban* I at a frequency of 40%; however, because *Ban* I was used only to discriminate white and striped marlin from sailfish in the ND4 identification key, this pattern did not affect the results (Figs. 1 and 2).

Nuclear marker

Six nuclear markers were screened in the preliminary analysis (Table 2). These included the short actin intron, the internal transcribed spacer (ITS) region (Goggin, 1994), and four anonymous single copy nuclear (scnDNA) markers. The scnDNA markers MN32-2, BM47, BM81, and WM08 were originally developed for analyses of popu-

lation structure in blue marlin (Buonaccorsi et al., 1999). The short actin intron primers were modified from "universal" actin gene primers "480" and "483" (Siddall et al., 2001).

Both the short actin and the ITS marker were rejected because neither marker amplified reliably across species. For the scnDNA markers, the program GeneJockey (Taylor, 1996) was used to search for the presence of restriction sites in sequences previously generated for blue marlin. The WM08 marker was screened with a total of ten enzymes, each of which produced identical patterns across species. BM47 and BM81 were also screened with ten enzymes each. For BM47, the combination of enzymes *Bcl* I and *Dde* I appeared to be diagnostic in a preliminary screening. However, upon further analysis, it was discovered that this combination of locus and enzymes produced confounding patterns for blue marlin and sailfish; the most common pattern for blue marlin was seen as a rare pattern for sailfish. Likewise, the BM81 locus did not distinguish between blue marlin and sailfish or between white and striped marlin and spearfish with any of the enzymes used. The MN32-2 locus was screened with a total of nine restriction endonucleases. The combination of *Dra* I and *Dde* I was found to allow for unambiguous identification of billfish species (Figs. 3 and 4).

As with the ND4 locus, after determining a diagnostic enzyme-locus combination, we screened a total of 540 billfish samples from a broad geographic range to evaluate the accuracy of the marker (Table 1). The enzyme *Dra* I was found to have two alternate alleles: "D" and "E" for blue marlin at a frequency of 19% and 5.5%, respectively. All other species appeared to be fixed for different (homozygous) alleles with respect to this enzyme. For *Dde* I, spearfishes had an alternate allele, "E," at a frequency of 36%. In addition, blue marlin had two alternate alleles "H" and "I" at frequencies of 16% and 40%, respectively (Table 4). Although the "H" allele in blue marlin was the only allele seen in black marlin, use of *Dde* I was not necessary to distinguish the two species since they are easily differentiated by *Dra* I (Figs. 3 and 4). All other species appeared to be homozygous for different alleles.

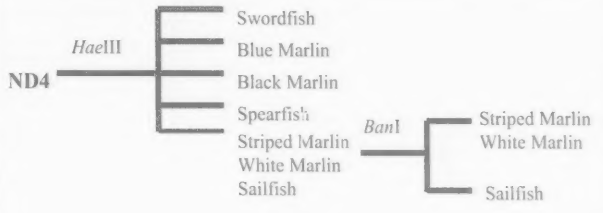

Figure 2

Key to distinguish species of billfishes based on the mitochondrial locus ND4.

Table 4

Restriction fragment patterns of the nuclear gene region BM32-2 of istiophorid billfishes. This locus did not amplify in the swordfish.

(**A**) Digestions with *Dra* I. A = blue marlin; B = striped marlin, white marlin, sailfish, black marlin; C = spearfish; D = blue marlin; E = blue marlin. A/D and A/E heterozygotes were seen in blue marlin cut with *Dra* I. Individuals of all other species were fixed homozygous.

A	B	C	D	E
650	640	640	650	1200
450	280	280	400	
	260	220	50	

(**B**) Digestions with *Dde* I. A = blue marlin; B = striped marlin, white marlin; C = spearfish; D = sailfish; E = spearfish; H = blue marlin; I = blue marlin. A/I A/H and H/I heterozygotes were seen in blue marlin cut with *Dde* I. C/E heterozygotes were seen in spearfish cut with *Dde* I. Individuals of all other species were fixed homozygous.

A	B	C	D	E	H	I
700	850	700	475	475	775	700
300	425	475	370	370	425	425
125		125	280	205		125
			130	125		

Discussion

The purpose of this study was to develop a key to the identification of billfish species based on independent mitochondrial and nuclear markers. Our goal was to make the process streamlined and capable of being performed in a modestly equipped genetics laboratory. Specific identification can be accomplished with a single PCR amplification of either the mitochondrial ND4 locus or nuclear MN32-2 locus and two restriction digestions. Previous methods with other mitochondrial gene regions have required the use of either four or 13 restriction digestions (Innes et al., 1998 and Chow 1994, respectively).

To facilitate specific identification, an objective of this study, was to develop diagnostic markers that exhibited limited intraspecific variation. Analysis of large sample sizes (60–100 or more) of sailfish, white marlin, striped marlin, blue marlin, and black marlin from throughout each species' range revealed minimal variation of the species-specific characters. Most species displayed a single genotype for digestions with the two enzymes used to cleave either the mitochondrial or nuclear amplification products, and no species exhibited more than three genotypes for any locus-restriction enzyme combination. In

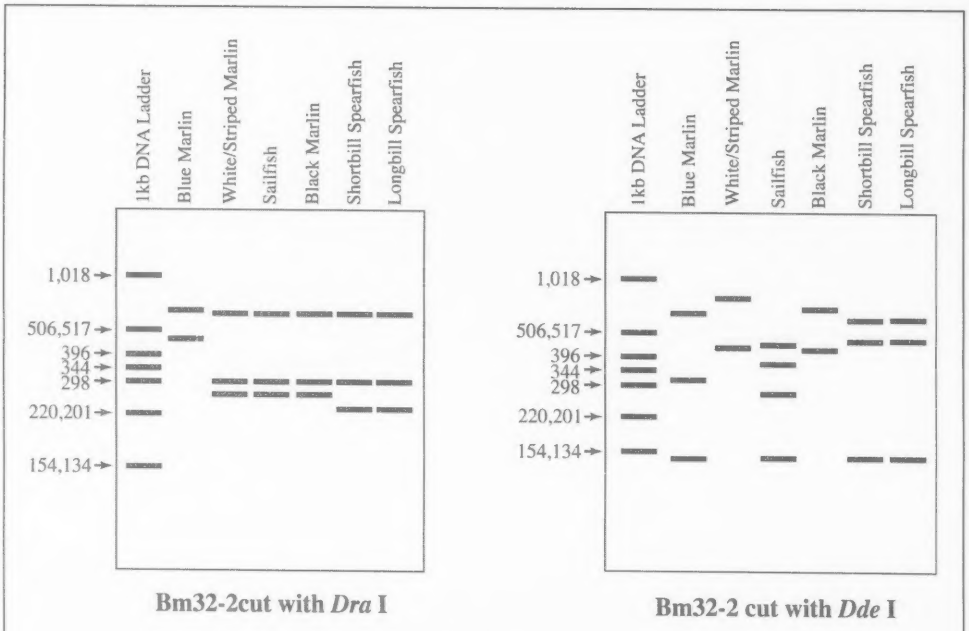

Figure 3

BM32-2 gel. Most common restriction fragment patterns of the nuclear gene region BM32-2 of istiophorid billfishes. This locus did not amplify in the swordfish. (**A**) Digestions with *Dra* I. From left to right, 1-kb DNA ladder, blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern B), black marlin (pattern B), shortbill spearfish (pattern C), and longbill spearfish (pattern C). (**B**) Digestions with *Dde* I. From left to right, 1-kb DNA ladder, blue marlin (pattern A), white and striped marlin (pattern B), sailfish (pattern D), black marlin (pattern H), shortbill spearfish (pattern C), and longbill spearfish (pattern C).

Figure 4

Key to distinguish species of billfishes based on the single copy nuclear locus MN32-2.

contrast, Innes et al. (1998) reported ten composite haplotypes among 47 black marlin, six composite haplotypes among 26 blue marlin, six composite haplotypes among 46 striped marlin, and six haplotypes among 21 swordfish, all from the southwest Pacific. From the level of intraspecific variation in relation to the sample sizes and the regional nature of their collections, it is reasonable to assume that Innes et al. (1998) may have missed several composite genotypes characteristic of the different species. In fact, from the level of variation exhibited by black marlin, striped marlin, and swordfish, Innes et al. (1998) suggested that their diagnostic species markers could be of potential use in population structure analyses. It occurs to us that if a genetic character exhibits sufficient intraspecific variation to be useful for analyses of stock structure, it is probably not a good candidate for species identification.

A high degree of genetic similarity was noted among white marlin and striped marlin in our study. None of the molecular markers evaluated in this study was able to unambiguously distinguish between the two species.

Figure 5

Larval billfish and its corresponding specific identification as a sailfish based on the BM32-2 locus. Lane 1 *Dra* I, lane 2, 1-kb plus DNA ladder (Gibco/BRL Life Technologies Inc., Bethesda MD), lane 3, *Dde I*.

Chow (1994) was also unable to distinguish between the two species based on RFLP analysis of the cytochrome *b* gene, and Innes et al. (1998) did not consider white marlin in their investigation because it does not occur in Australian waters. RFLP analysis of the whole mtDNA molecule indicated that white and striped marlin share composite haplotypes, although there are highly significant frequency differences between the species (Graves and McDowell, 1995; Graves, 1998). Sequence analysis of the mtDNA cytochrome *b* gene also demonstrated a lack of genetic divergence among white and striped marlin (Finnerty and Block, 1995), and a further genetic analysis of the species' relationships is warranted.

To evaluate the utility of the methods outlined in our study with those of other investigators, detailed protocols and six unknown billfish samples were sent to the Southeast Fisheries Science Center's (now National Ocean Survey's) Charleston, SC, laboratory. Scientists at the Charleston Laboratory analyzed both mitochondrial and nuclear DNA markers for each sample and arrived at consistent, correct identifications for each of the samples of unknown billfish. In addition, samples of juvenile billfish collected by investigators at the University of Miami were analyzed in our laboratory with these molecular markers. Samples consisting of one eye taken from a 3-mm juvenile billfish provided sufficient DNA to amplify the mtDNA and nuclear markers, allowing specific identification (Fig. 5). The technique is currently being used to determine the temporal occurrence of istiophorid larvae in the Florida Straits (Luthy and McDowell[2]).

Although the methods presented in our study allow the specific identification of billfish species, more sensitive molecular markers are required to distinguish among ocean populations of some istiophorid species. Amendment I to the Fishery Management Plan for Atlantic Billfishes prohibits the sale of blue marlin, white marlin, and sailfish taken in the Atlantic Ocean, although it is legal to market blue marlin, striped marlin, and sailfish from the Indian or Pacific oceans. Enforcement of this regulation requires the ability to discriminate between Atlantic and Indo-Pacific individuals of blue marlin, sailfish, and white and striped marlin. Examination of our results suggests that there are several other molecular markers, which while not used in this study, occur at relatively high frequencies in Atlantic blue marlin, sailfish, and white marlin but do not occur in their Pacific conspecifics. These molecular markers could potentially be used to identify some Atlantic individuals without misclassifying a Pacific fish, thereby allowing the enforcement of the management plan. Additional work will be required to develop a database that would support such analyses.

[2] Luthy, S., and J. McDowell. 2001. A molecular approach to the identification of larval billfishes. Submitted to the Australian Journal of Marine and Freshwater Research as part of the 3rd international billfish symposium. CSIRO Publishing, 150 Oxford St. Collingwood, Vic. 3066, Australia.

Acknowledgments

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Seasonal growth of King George whiting (*Sillaginodes punctata*) estimated from length-at-age samples of the legal-size harvest

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Abstract—Samples of 11,000 King George whiting (*Sillaginodes punctata*) from the South Australian commercial and recreational catch, supplemented by research samples, were aged from otoliths. Samples were analyzed from three coastal regions and by sex. Most sampling was undertaken at fish processing plants, from which only fish longer than the legal minimum length were obtained. A left-truncated normal distribution of lengths at monthly age was therefore employed as model likelihood. Mean length-at-monthly-age was described by a generalized von Bertalanffy formula with sinusoidal seasonality. Likelihood standard deviation was modeled to vary allometrically with mean length. A range of related formulas (with 6 to 8 parameters) for seasonal mean length at age were compared. In addition to likelihood ratio tests of relative fit, model selection criteria were a minimum occurrence of high uncertainties (>20% SE), of high correlations (>0.9, >0.95, and >0.99) and of parameter estimates at their biological limits, and we sought a model with a minimum number of parameters. A generalized von Bertalanffy formula with t_0 fixed at 0 was chosen. The truncated likelihood alleviated the overestimation bias of mean length at age that would otherwise accrue from catch samples being restricted to legal sizes.

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In this study, we estimated growth curves from six data sets of fish sampled from the commercial and recreational catch of an important fish species in South Australia (Fig. 1), King George whiting (*Sillaginodes punctata*). Like many temperate fish populations, recruitment and growth can be assumed to follow a yearly cycle. A variety of methods have been used to measure seasonal variation in fish growth including mark-recapture (Francis, 1988; Coggan, 1997) and otolith annulus-diameter increments in combination with tetracycline marking (Panfili et al., 1994; Fabré and St. Paul, 1998; Francis et al., 1999). The method used in our study is the most widely employed, of fitting to lengths-at-age, where the age of each sampled fish is read as a count of yearly otolith annuli from samples of the harvest.

The model-fitting algorithm had three key objectives, each to represent a specific feature of the growth of South Australian King George whiting, or of the data set. These were expressed mathematically as deviations from a standard 3-parameter von Bertalanffy model fitted with a normal likelihood.

The first two objectives were elaborations on the standard von Bertalanffy growth curve (understood as a deterministic function of mean length versus age). The first objective was to make seasonality explicit in the growth curve (Pitcher and MacDonald, 1973; Somers, 1988; Hoenig and Hanumara, 1990; Pauly and Gaschütz[1]) and the second objective was to allow a wider range of curvatures by using the *r*-exponent (Schnute, 1981).

For application of this growth description in length- and age-based stock assessment modeling, we also estimated the shape of the length-at-age probability density function (pdf), which quantifies the distribution of fish of different lengths at each age.

The principal regulation of both recreational and commercial King George whiting harvest is by legal minimum length (LML); fish smaller than the LML cannot be landed and must be returned to the sea. Therefore fish obtained from the catch are a biased sample. The third objective was to explicitly account for the absence of fish below the LML, for which a truncated pdf was used. This truncated normal density, the pdf of observed lengths-at-age, was also used as the likelihood for each individual sample.

A range of models were examined that met these three objectives. These included a seasonal version of the Richards (1959) model proposed by Akamine (1993), which makes different use of the *r*-exponent. Therefore a fourth objective was to apply standard statistical model selection techniques. Methods to choose the most appropriate model for a given growth data set were reviewed by Quinn and Deriso (1999). Hierarchical model fits are statistically comparable using their likeli-

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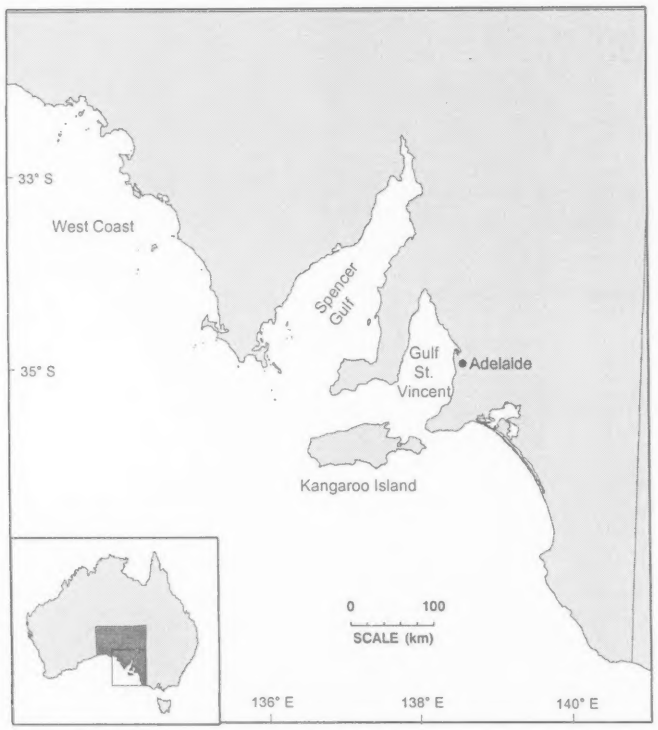

Figure 1

South Australian coastal waters. King George whiting (*Sillaginodes punctata*) are found predominantly in the two Gulfs, and along the West Coast.

hood ratio (Kimura, 1980; Rice, 1995). We sought to reduce the original 8-parameter model and employed likelihood ratio tests to evaluate the relative fit of the simpler models tested. We specify and apply a set of selection criteria below, seeking one common model form for six data sets to describe the length-at-age distributions. A 7-parameter generalized seasonal von Bertalanffy model, with t_0 fixed at zero, was chosen.

In addition, we applied an allometric relationship (a power curve) to fit weight versus length for this population.

That the samples are not uniform by length in commercial catch is common to most fisheries. The absence of fish below LML or below the lengths selected by the fishing gear, inevitable when sampling is from the landed catch, creates an overestimation bias of mean length-at-age, because faster growing fish reach the legal stock sooner and are thus over-represented in those samples. This sampling bias was taken into consideration by the use of a truncated model likelihood assuming zero probability of capture below legal size. In practice, the clear advantage of samples from the landed (commercial or recreational) harvest is a substantially lower cost than the alternative of fishery-independent samples gathered, usually by researchers, at sea.

The specific length-dependent bias in sampling changed during the time of the study. The LML was raised from 280 mm to 300 mm. Also, some of the samples were gathered by researchers who landed all, notably smaller fish. By applying one of three different likelihoods to any given sample, having different truncation lengths of 280 mm, 300 mm, or no truncation, all fish samples were combined in a single length-at-age estimation for each of three regional subpopulations, and by sex.

Materials and methods

A total of 11,164 King George whiting were sampled between 1995 and 1998 from across the main fishery area of South Australia. Most samples were obtained by subsampling the commercial catch at local fish processing plants or by purchasing fish from commercial processors. Some samples were provided as frozen fish frames (fillets removed) by recreational fishermen, and the remainder were caught on scientific cruises. Each fish was measured for total (TL) and standard lengths (SL) to the nearest mm, and weighed to 0.1 g. Gonads were removed, sexed, and weighed. The sagittae, the largest pair of otoliths, were removed from each fish for age determination.

Samples were subdivided into six data sets: three spatial regions and by sex (Table 1). Movement studies based

Table 1

Summary of data sets, each fish measured for age, length, and weight in the King George whiting analysis. Samples from commercial and recreational fisheries were regulated by a 280-mm legal minimum length (LML) before 1 September 1995, a 300-mm minimum length thereafter.

Area	Area abbreviation	Sex	Beginning date	End date	Sample size: Researchers	Sample size: Fisheries 280 LML	Sample size: Fisheries 300 LML
Gulf St. Vincent and nortern Kangaroo Island	GSV	male	4 Aug 94	17 Feb 99	293	503	1139
		female	4 Aug 94	17 Feb 99	373	615	1343
Spencer Gulf	SG	male	23 Apr 94	30 Sep 97	267	298	924
		female	23 Apr 94	30 Sep 97	363	441	1300
South Australian West Coast	WC	male	27 Apr 94	18 May 97	167	805	608
		female	27 Apr 94	19 May 97	226	857	642

on tag recoveries over three decades (Fowler and March[2]) indicated three largely self-sustaining subpopulations: Gulf St. Vincent, Spencer Gulf, and West Coast (Fig. 1).

Young fish (two- and three-year-olds) were aged by interpretation of the macrostructure of the whole sagittae. For fish with more complex otoliths, the otolith was snapped in two across the posterior-anterior axis through the center, exposing the transverse face of both halves. One of these halves was burnt in a bunsen flame and then examined with a binocular dissecting microscope at 6–20× magnification. The surface being examined was smeared with immersion oil. The alternating opaque and translucent zones were counted. The periodicity of formation of this macrostructure in sagittae of King George whiting has been validated and the following algorithm was developed for conversion of ring count to age (Fowler and Short, 1998):

$$a = 12N + m_b + m_c,$$

where a = age in months;
N = number of opaque zones;
m_b = 8 = number of months from universal birth date (i.e. 1 May) midway through spawning season to the end of the year; and
m_c = number of months from the start of year to the month of capture.

Some samples of fish were scaled in the commercial processing plant prior to weighing and measuring for length. Although this process did not affect their lengths, it did result in an appreciable loss of weight. Consequently, for estimation of weight-length relationships we corrected the weights of scaled fish using a linear relationship that was derived by weighing 155 fish before and after scaling. This linear relationship was

$$(corrected\ weight) = 1.0176 \times (scaled\ weight) + 3.5835\ (r^2=0.99, P<0.001, \mathrm{df}=154).$$

Growth: length-at-age

In order to make explicit the absence of fish samples smaller than LML, a truncated normal probability density function of length was used to describe the probability of capture of individual fish in each monthly age. This pdf was employed as the likelihood of observation of each individual, given its age. Truncation implies a zero predicted probability of observing a commercially or recreationally sampled fish less than LML. A few sublegal fish were measured and, being unrepresentative, were removed from the six data sets.

During the period of sampling, in September 1995, the regulated size of LML for commercial and recreational fishery samples was increased from 280 to 300 mm. The likelihood truncation length was thus a function of date of capture. This necessitated two forms of likelihood, for LMLs of 280 and 300 mm. Smaller numbers of samples obtained on scientific cruises were not subject to LML size controls. Thus a third, regular untruncated, likelihood was used to model research samples.

A normal likelihood was fitted to model the distribution of lengths at each age:

$$L = \frac{1}{\sqrt{2\pi}\,\sigma(a_i)} \exp\left[-\frac{1}{2}\left\{\frac{l_i - \bar{l}(a_i)}{\sigma(a_i)}\right\}^2\right], \qquad (1)$$

where l_i = length of fish sample i; and
a_i = age of fish sample i obtained from count of its otolith annuli.

[2] Fowler, A. J., and W. A. March. 2000. Adult movement patterns. *In* Development of an integrated fisheries management model for King George whiting (*Sillaginodes punctata*) in South Australia (A. J. Fowler and R. McGarvey, eds.), p. 83–104. FRDC Final Project Report 95/008. Fisheries Research and Development Corporation, PO Box 222, Deakin West ACT 2600, Australia.

The mean length-at-age

$$\bar{l}(a_i) = L_\infty\left\{1-\exp\left[-K\left\langle\frac{a_i-t_0}{12}+\frac{u}{2\pi}\left\{\begin{matrix}\sin(2\pi(a_i-\omega)/12)-\\ \sin(2\pi(t_0-\omega)/12)\end{matrix}\right\}\right\rangle\right]\right\}^r. \quad (2)$$

was modeled by a seasonally periodic von Bertalanffy growth formula, generalized by the inclusion of an exponent, r. Age (a_i) was in integral units of months, with May, the assumed date of birth at mean time of spawning of South Australian King George whiting, being month 1. Division by 12 in the mean length formula preserves the usual units of K where age is in years.

The seasonality function is sinusoidal, although more complex seasonality functions can be postulated that allow asymmetry in growth through the year. Values of the seasonality amplitude parameter $u > 1$ imply decreasing length in the yearly time of minimum growth (Pauly and Gaschütz[1]). We therefore constrained $u \leq 1$, assuming that no shrinking in length occurs. With sine, the phase parameter (ω) gives the month of maximum growth, where months of age 1, 13, 25, etc. denote the birth month, May.

The likelihood standard deviation (σ) was modeled as an allometric function of mean length:

$$\sigma(a_i) = s_0 \cdot \left(\bar{l}(a_i)\right)^{s_1}. \quad (3)$$

This power function for standard deviation in terms of mean length, applied by Francis (1988) to fitting tag-recovery length increments, has the desired property that once growth stops, the standard deviation in lengths-at-age also ceases to change. Similarly, in winter months of slowed (or zero) mean length increase, change in standard deviation slows correspondingly.

The left-truncated normal likelihood, which applies to samples from commercial and recreational fishermen,

$$L_i = \begin{cases} \dfrac{1}{\sigma(a_i)}\exp\left[-\dfrac{1}{2}\left\{\dfrac{l_i-\bar{l}(a_i)}{\sigma(a_i)}\right\}^2\right] \Bigg/ \\ \left\{\displaystyle\int_{LML_i}^{+\infty}\frac{1}{\sigma(a_i)}\exp\left[-\frac{1}{2}\left\{\frac{l-\bar{l}(a_i)}{\sigma(a_i)}\right\}^2\right]dl\right\}, \text{ if } l_i \geq LML_i \\ 0, \text{ if } l_i < LML_i \end{cases} \quad (4)$$

postulates a probability cut-off to zero for landed samples less than LML and a normal probability, integrating to 1, for the range of legal lengths. LML is subscripted by the fish sample data point (i) to indicate that LML is either 280 or 300 mm depending on the date of capture of the fish. For research samples, for which all lengths could be observed, the full untruncated normal likelihood (Eq. 1) was used.

Parameters were estimated by minimizing the negative sum of log-likelihoods with the AD Model Builder estimation software (Otter Research Ltd., Sidney, B.C., Canada):

$$O = -\sum_{i=1}^{n}\ln(L_i). \quad (5)$$

Initial parameter values for all models tested were $t_0 = 0$, $u = 1$, $\omega = 9$, $s_0 = 0.1$, $s_1 = 1$, $r = 1$, with $L_\infty = 480$, $K = 0.36$ for females, and $L_\infty = 420$, $K = 0.6$ for males.

Confidence bounds on parameters for each data set were derived by assuming the standard asymptotic normal approximation. These were numerically calculated by AD Model Builder routines as the diagonal elements of the covariance matrix, the negative inverse of the Hessian matrix at the likelihood maximum.

Growth model choice

The full, seasonal, generalized von Bertalanffy model described above has eight parameters. A best-fitting model with the minimum number of parameters was sought. In cases where a model is overparameterized, high correlations between parameters appear and the confidence bounds widen. To test for a diagnosis of overparameterization and then to correct it by fixing otherwise freely estimated parameters, we applied the following algorithm based on standard methods of model selection:

1 Search for parameters that frequently show high correlations with other parameters, have high variances, or in estimation hit preset upper and lower bounds, beyond which biologically unrealistic values are being inferred.
2 Set those parameters to fixed likely values. This assumes a biologically likely value can be postulated. If not, use a mean value among the range of estimates obtained when the parameter is allowed to vary freely. A parameter may also be selected if it varies little among the range of data sets for which estimates are obtained.
3 Test for the change in negative log-likelihood to determine whether the reduced model is significantly less well fitting by using chi-square likelihood ratios.
4 Check that confidence intervals and correlations are reduced.

In addition, we seek model that converges reliably for all data sets. Satisfactory convergence should not depend on the initial parameter values chosen, but in some cases a new set of initial values can be tried for any given nonconverging data set. Convergence can also depend on the minimization algorithm or subroutine employed. However, for purposes of model selection, failure to converge for some data sets analyzed is an indication that the likelihood surface for that model is less smooth and the true global maximum may not always be obtained. Reliable convergence is particularly desirable when 1) bootstrapping, where nonconvergence leaves resampled data sets

unestimated, and 2) for integration of growth into overall fishery stock assessment estimators, where finding more appropriate initial values for the growth parameters may be nontrivial, and the cause of nonconvergence of the overall estimation may not be easily traced to the growth submodel.

In addition to reduced versions of the model presented above, we fitted a related model proposed by Akamine (1993), which incorporates into the Richards (1959) growth curve a sinusoidal seasonality function like that of Equation 2.

Weight-at-length

Mean (corrected) weight versus total length was modeled by an allometric relationship:

$$\overline{w}(l_i) = \alpha l_i^{\beta} \tag{6}$$

A normal likelihood was again used. The standard deviation of the likelihood (i.e. of the fitted spread of observed weights about the mean given in Eq. 6) was assumed to vary linearly with length:

$$\sigma_w(l_i) = \sigma_{w0} + \sigma_{w1} l_i, \tag{7}$$

Parameter confidence bounds were estimated by a bootstrap of 1000 runs.

Results

Growth model choice

The generalized von Bertalanffy model (Eq. 2, abbreviated as gVB) gave the best fit with five of six data sets (Table 2). However for both gVB and the other 8-parameter model, Akamine-Richards (AR), correlations among parameters were unacceptably frequent and high (Table 2). Other evidence of overparameterization included frequent occurrence of wide confidence bounds (SE >20%, Table 2). High correlations and parameter uncertainties were most widespread for s_0 and s_1. The exponent, r, and seasonality amplitude, u, also occurred frequently with high uncertainty, and t_0 and r often were found in high correlations; t_0 hit both upper (7.99) and lower (–30) confidence bounds for some models with west coast data sets. As with standard von Bertalanffy models, t_0 quantifies the age (here, in months) at which length extrapolates to 0. The occurrence of u estimates hitting their upper bound of 1 is not due to model overparameterization but reflects the biological modeling decision to exclude shrinking.

The Akamine-Richards (AR) model varied widely among data sets in its relative closeness of fit, failed to converge for West Coast females, and did not yield a positive definite hessian for Gulf St. Vincent females. It was less well fitting than the gVB for all but one data set. The gVB model was therefore chosen as the better 8-parameter model, and subsequent reduced models were based on it in preference to AR.

From indicators summarized above, four parameters for defining overall mean length K, L_∞, t_0 and r, appear to be too many. Two obvious candidates for fixing to constant values were t_0 and r. These occurred frequently in indicators of model overparameterization. Both have intuitive biological default values at which they can be fixed, 0 and 1 respectively. Thus two 7-parameter models were run, with t_0 and r fixed, the latter (with r=1) reducing to a seasonal von Bertalanffy curve (Somers, 1988; Hoenig and Hanumara, 1990).

The fit with $t_0 = 0$ fixed was not significantly different from the full 8-parameter gVB for three of six data sets. This fit was tested by chi-square likelihood ratios at 95% confidence, indicated (Table 2) by successive likelihood-ratios of 1.92 or less, for comparing fits of hierarchical models differing by one in number of freely estimated parameters (Rice, 1995). The regular seasonal von Bertalanffy model (r=1, abbreviated as "reg VB") fitted less closely than gVB with $t_0 = 0$ for all six data sets; significantly worse for all Spencer Gulf and West Coast data sets. In addition, not shown in Table 2, the estimates of t_0 were frequently far from the realistic biological range near 0, often estimated at 10 to 20 months above or below. The frequency and magnitude of high correlations were substantially reduced with both 7-parameter models. Thus we choose to fix $t_0 = 0$ and let r freely vary.

The occurrence of very high correlation between s_0 and s_1 for all data sets and models (Table 2) suggested fixing one of them, in particular, the exponent, s_1. We set $s_1 = 0.3$ which fell near the average among the range of estimated values. The outcome was that t_0 (now free) hit its bound in three of six cases, thus exacerbating that pathology. When both $t_0 = 0$ and $s_1 = 0.3$ were fixed, the fits were uniformly poor (Table 2). Thus, the high correlation between the two allometric standard deviation parameters met with no obvious solution. However, these posed no wider problem because these parameters did not interact with those describing the mean length at age and the correlation between pairs of allometric parameters (such as α and β in the weight-length model, Eq. 6) is common and often unavoidable. Because a significantly better fit for the length-at-age standard deviation is sought, we let both s_0 and s_1 vary freely.

The gVB with $t_0 = 0$ fixed provided an optimal trade-off in reduced overparameterization and good fit: it achieved the objective of substantially reduced interparameter correlations without significantly worse fits in three of six cases. The remaining three data sets (Spencer Gulf females and males, West Coast females) had yielded unrealistic estimates of t_0 in full model gVB (of –17.9, –21.7, and the upper bound of 7.99 respectively). This model was therefore chosen and results from it presented below.

Growth: length-at-age

Estimated length at age showed seasonal periodic trends for the three regions and two sexes (Figs. 2–4). Estimates of u (seasonality amplitude) were constrained at the maximum allowed value of $u = 1$ for three of six data sets (Table 3). The peak month of maximum growth occurred in mid-

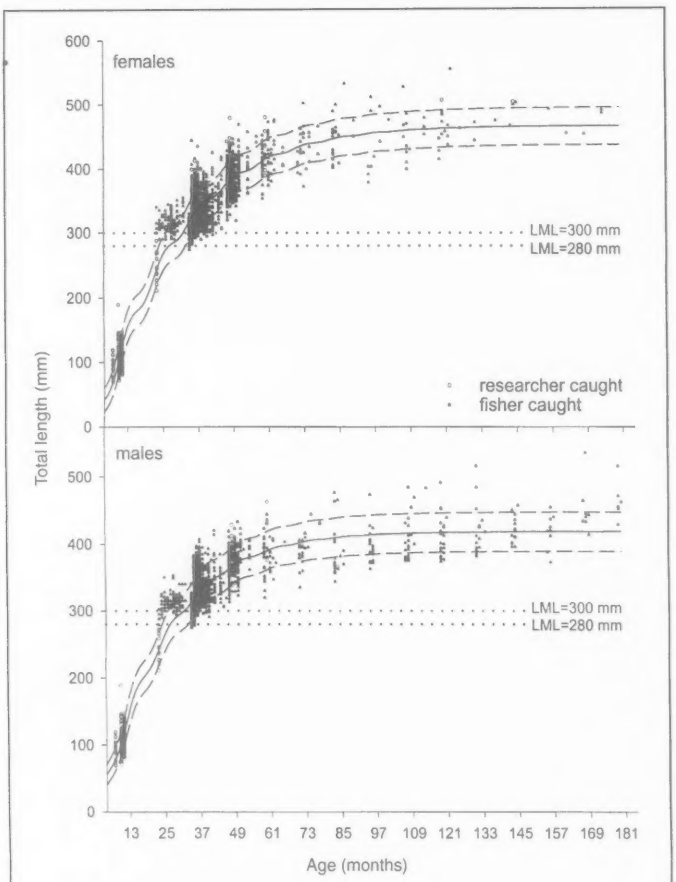

Figure 2

Lengths at age, beginning at 10 months, for Gulf St. Vincent King George whiting of both sexes. The solid line is the generalized seasonal von Bertalanffy mean length curve (Eq. 2) with $t_0 = 0$ fixed. Dashed lines indicate confidence bounds as normal likelihood standard deviation (Eq. 3). Dots represent individual observations of length-at-age.

summer (December–February) for all data sets except Gulf St. Vincent males.

Estimated (likelihood maximum) and observed distributions of lengths-at-age were plotted for Gulf St. Vincent females (Fig. 5) and males (Fig. 6). Because the estimation likelihood was fitted to formulas for mean (Eq. 2) and standard deviation (Eq. 3) of all ages at once, close fit to the majority of individual length-at-age distributions indicated a growth description mutually consistent among ages and a satisfactory approximation to monthly lengths at age overall.

For younger ages (28–35 months), the sampled frequencies were modeled by the truncated right-hand component of the normal pdf. The LML truncation lengths for each normal curve (280 or 300 mm in Figs. 5 and 6) indicated the lower limit of samples from the fishery. These samples are generally well fitted (Figs. 5 and 6), suggesting these truncated younger samples do contribute to the overall growth fit and that the truncated likelihood is effective in describing the monthly growth of the length-at-age cohort across LML into legal sizes. One exception yielding a less close fit were female fish aged 28 months taken under a LML of 280 mm (Fig. 5).

Weight-at-length

Parameter estimates for α and β (Eq. 6) covaried strongly. When all four parameters were allowed to freely vary, β differed little from 3.2 for all data sets (Table 4). Likelihood-ratio tests were therefore carried out to determine whether the model allowing β to vary freely yielded significantly better fits than one with three parameters and β fixed at 3.2. For all but Spencer Gulf males, likelihood-

Table 2

Criteria for model selection. gVB = generalized von Bertalanffy (Eq. 2); AR = Akamine-Richards (Akamine, 1993). Reduced gVB models fixed t_0 at 0 and s_1 at 0.3. Models in each data set are given in order of best to worst fitting. Differences in –logL provide likelihood ratio (L-ratio) test comparisons of the goodness of fit of successively reduced hierarchical models. An L-ratio of 1.92 (3.0) or greater implies a significantly better fit at 95% under a chi-square likelihood ratio test by comparison with reduced models of one (two) fewer parameters. High correlations between pairs of parameters are shown for three arbitrary categories: ** = >0.99; * = 0.95–0.99; pairs in this column unmarked by an asterisk had correlations of 0.9–0.95.

Data set	Model	No. of parameters	–logL	Successive L-ratios	Parameter pairs with |cors|>0.9	Parameters with SE/estimate > 0.2	Parameters hitting estimation bound
Gulf St. Vincent females	gVB	8	10566.63		t_0~r**; t_0~K; r~K; s_1~s_0**	u, r, s_0, s_1	
	gVB t_0=0	7	10568.09	1.45	r~K; s_1~ s_0**	u, s_0, s_1	
	gVB t_0=0 & s_1=0.3	6	10570.38	2.29	r~K	u	
	reg VB	7	10571.27	0.89	L_∞~K; s_1~ s_0**	u, s_0, s_1	
	AR	8	10575.67	4.39	Hessian not positive definite	—	
Gulf St. Vincent males	gVB	8	8632.695		t_0~r**; t_0~K*; ω~K; s_1~ s_0**; t_0~ω*;r~K*; r~ω	u, r, s_0	
	AR	8	8632.695	0.00	t_0~r**; t_0~K*; r~K; s_1~ s_0**; t_0~ω*;ω~K;r~ω	u, r, s_0	
	gVB t_0=0	7	8632.759	0.06	r~K; s_1~ s_0**	u, s_0	
	reg VB	7	8632.908	0.15	t_0~u; s_1~ s_0**	u, s_0	
	gVB t_0=0 & s_1=0.3	6	8637.379	4.47	Hessian not positive definite	u	
Spencer Gulf females	gVB	8	9374.685		t_0~K; r~K; r~ t_0**; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0	7	9391.099	16.41	K~ L_∞ r~K; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0 & s_1=0.3	6	9392.176	1.08	K~ L_∞; r~K		
	AR	8	9420.834	28.66	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	9429.822	8.99	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
Spencer Gulf males	gVB	8	6620.955		t_0~r; s_1~ s_0**	r, s_0, s_1	u=1
	gVB t_0=0	7	6661.097	40.14	r~K; s_1~ s_0**	s_0, s_1	u=1
	AR	8	6728.644	67.55	K~ L_∞; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	6729.238	0.59	s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0 & s_1=0.3	6	7230.275	501.04	r~K	u	
West Coast females	AR	8	7771.561		K~ L_∞; r~ L_∞**; r~K*; s_1~ s_0**	s_0, s_1	t_0=-30
	gVB	8	7798.542	26.98	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	gVB t_0=0	7	7805.209	6.67	K~ L_∞; r~K; s_1~ s_0**	s_0, s_1	u=1
	reg VB	7	7819.477	14.27	K~ L_∞*; s_1~ s_0**	s_0, s_1	u=1, t_0=7.99
	gVB t_0=0 & s_1=0.3	6	7828.671	9.19	K~ L_∞; r~K*	u	
West Coast males	gVB	8	7011.73		r~K*; s_1~ s_0**	u, s_0, s_1	t_0=7.99
	gVB t_0=0	7	7013.403	1.67	r~K*; r~u; s_1~ s_0**	u, r, s_0, s_1	
	reg VB	7	7083.513	70.11	K~ L_∞*; s_1~ s_0**		t_0=7.99
	gVB t_0=0 & s_1=0.3	6	7828.671	745.16	r~K*; r~u	u, r	
	AR	8	failed to converge	—			

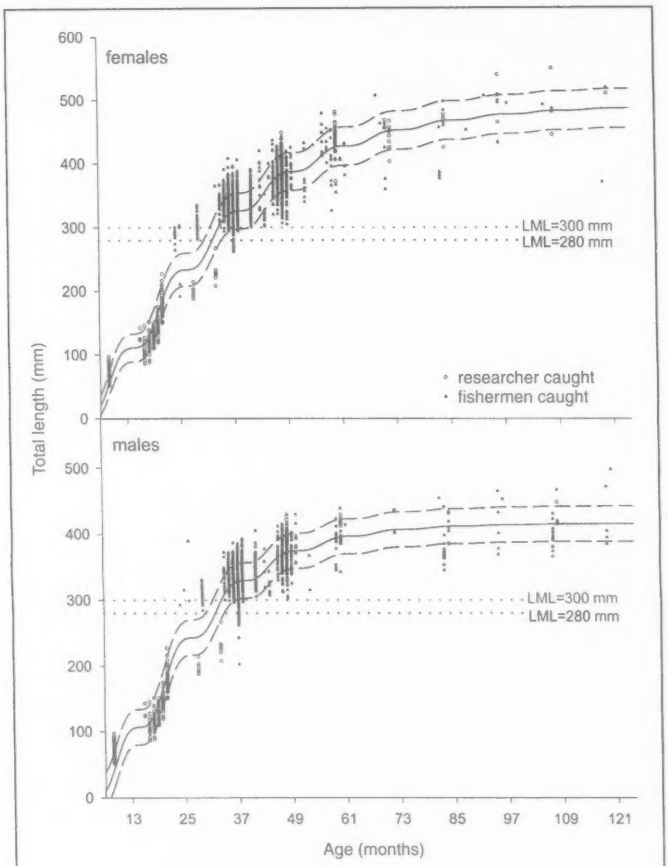

Figure 3

Lengths versus age of King George whiting sampled from Spencer Gulf, plotted as in Figure 2.

ratio tests showed that β did not differ significantly from 3.2 (Table 4). With $\beta = 3.2$ fixed, values of α among the six data sets differed little (Table 5, Fig. 7).

Discussion

In this study we estimated parameters of length at age for six data sets, comparing the fits of different models by using four standard diagnostic tools, notably likelihood ratios, correlations, standard errors, and parameter estimates among data sets either varying widely or varying little, to evaluate the estimators being compared. Similarly, for weight versus length in the same population, we assessed six data sets, and used likelihood ratio to compare model fits. For both length at age and weight versus length, the diagnostic analysis suggested the initial full models were overparameterized and indicated which parameters should be fixed and what values.

Likelihood ratio tests allow comparisons only between hierarchical models, that is in comparing full and reduced models, the latter a subcase of the full model obtained by fixing one or more parameters in the full model. In the case of generalized von Bertalanffy and Akamine-Richards, setting $r = 1$ yielded the same model, namely seasonal von Bertalanffy. The other two reduced models analyzed (gVB with t_0=0 and with both t_0=0 and s_1=0.3) were reduced models only of generalized von Bertalanffy. Although other comparison tests are possible for hierarchical models (Quinn and Deriso, 1999), the Neyman Pearson lemma assures that in the situation where it applies, the likelihood-ratio test is optimal in that it yields the most powerful test for any given choice of significance level, α (Rice, 1995).

Fits of nonhierarchical models can be compared by using the Akaike or Bayes information criteria (Quinn and Deriso, 1999). Fournier et al. (1998) applied the Aitkin posterior Bayes factors for hypothesis model comparisons in

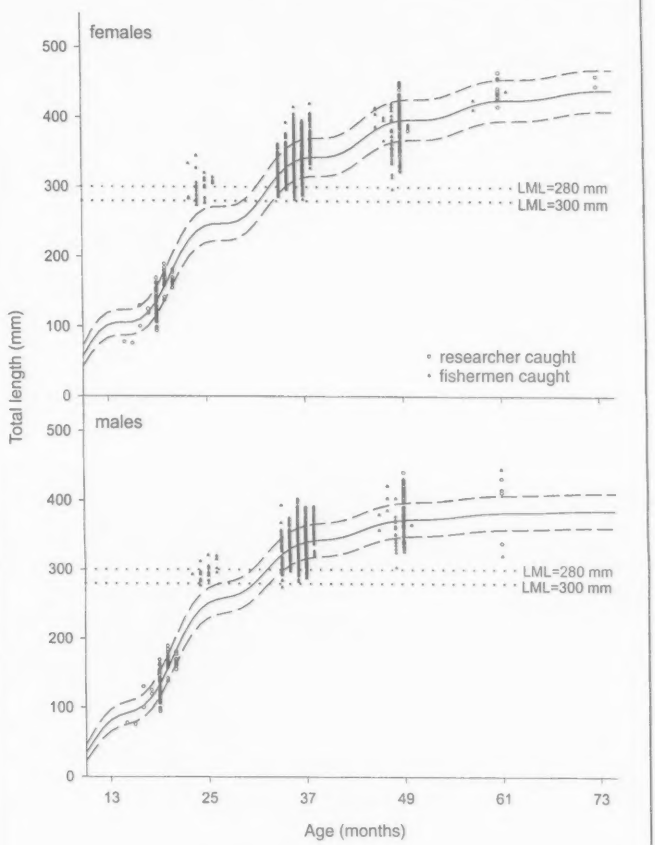

Figure 4

Lengths at age for the South Australian West Coast, plotted as in Figure 2.

a Bayesian context. Recently, Buckland et al. (1997) have proposed averaging the estimates from the range of models examined, weighting each estimate by functions of the Akaike or Bayes information criteria. This mitigates the need to choose one specific model as we have done, and like the Akaike or Bayes criteria, applies to nonhierarchically related models. However, in situations where the growth model will be incorporated into a larger stock assessment estimation, a range of growth submodels would be challenging to implement. Moreover in cases where evidence of overparameterization is given, a reduced-parameter model can reduce both bias and the influence of sample variation.

Sinusoidal seasonality (Pauly and Gaschütz[1]) was represented in a now standard way that preserves the interpretation of t_0 as the age at which length equals zero (Somers, 1988; Hoenig and Hanumara, 1990). Pawlak and Hanumara (1991) showed that this form of seasonality model yielded statistical advantage. Hyndes et al. (1998) aged samples of King George whiting in southwestern Australia that grew faster and reached larger maximum lengths than those from South Australia. The analysis of Hyndes et al. (1998) did not describe the distribution of lengths-at-age or consider seasonality, which was less evident in their plotted data.

The exponent, r, allowed nonlinear variation away from the strict von Bertalanffy form. With the South Australian King George whiting data sets, it improved the model description; fitted r's ranged from 1.25 to 4.59, outside the range describable by the unmodified seasonal von Bertalanffy model where implicitly $r = 1$ fixed.

We are not aware of previous attempts to use a truncated likelihood in an age-based description although Smith and Botsford (1998) applied size truncation in fitting a von Foerster equation to length samples. Truncation proved effective in alleviating this potential large source of bias. The extent of the bias is evident in the growth curve scatterplots (notably Figs. 2 and 4) where large numbers of

Table 3

Length-age parameters and derived estimates (with t_0=0 fixed). The 95% confidence intervals shown in parentheses are 1.96 times the asymptotic standard error; for strictly positive parameters, these are shown as percentages of the estimate value.

	Gulf St. Vincent		Spencer Gulf		West Coast	
Parameter	females	males	females	males	females	males
L_∞	467.0 (±1.5%)	418.4 (±1.1%)	492.6 (±2.2%)	416.1 (±1.5%)	454.4 (±3.2%)	387.0 (±2.8%)
K	0.48 (±6.4%)	0.61 (±5.8%)	0.49 (±6.9%)	0.77 (±6.6%)	0.70 (±9.4%)	1.17 (±15%)
u	0.59 (±41%)	0.46 (±68%)	1 (±0.05%)	1 (±0.08%)	1 (±0.14%)	0.79 (±57%)
ω	–1.55 (Feb) (±0.77)	24.0 (Apr) (±0.004)	8.50 (Dec) (±0.32)	8.67 (Dec) (±0.39)	8.96 (Dec) (±0.42)	9.02 (Jan) (±0.59)
s_0	8.97 (±58%)	4.17 (±47%)	7.34 (±52%)	27.6 (±53%)	3.53 (±96%)	3.93 (±100%)
s_1	0.19 (±0.10)	0.32 (±0.082)	0.23 (±0.091)	-0.005 (±0.095)	0.35 (±0.17)	0.31 (±0.17)
r	1.25 (±6.9%)	1.41 (±7.8%)	1.66 (±6.9%)	2.35 (±9.8%)	2.33 (±11%)	4.59 (±40%)

Table 4

Likelihood-ratio tests comparing differences in the fits between weight-length models which allow β to vary and those which kept $\beta = 3.2$ fixed. Significant difference is indicated by $P < 0.05$.

	Gulf St. Vincent		Spencer Gulf		West Coast	
	females	males	females	males	females	males
β-estimate (free to vary)	3.200255	3.200008	3.200031	3.198721	3.200050	3.200021
L-ratio statistic	0.677	0.000	0.005	6.094	0.033	0.006
P-significance (models differ)	0.41	0.99	0.94	0.01*	0.86	0.94

Table 5

Weight (g) versus length (mm TL) parameters from Equation 6 and derived estimates with $\beta = 3.2$ fixed. 95% confidence intervals are 1.96 times the bootstrap standard deviation over 1000 runs given in parentheses as percentages of the estimate value.

	Gulf St. Vincent		Spencer Gulf		West Coast	
Parameter	females	males	females	males	females	males
α	$1.858–10^{-6}$ (±0.51%)	$1.874–10^{-6}$ (±0.63%)	$1.880–10^{-6}$ (±0.77%)	$1.888–10^{-6}$ (±0.87%)	$1.861–10^{-6}$ (±0.40%)	$1.887–10^{-6}$ (±0.32%)
β	3.2	3.2	3.2	3.2	3.2	3.2
$\sigma_{\omega 0}$	–7.76 (±15%)	–6.74 (±12%)	–6.94 (±13%)	–5.21 (±24%)	–6.38 (±13%)	–6.32 (±6.2%)
$\sigma_{\omega 1}$	0.094 (±8.0%)	0.080 (±7.2%)	0.087 (±12%)	0.078 (±19%)	0.067 (±8.0%)	0.063 (±4.6%)

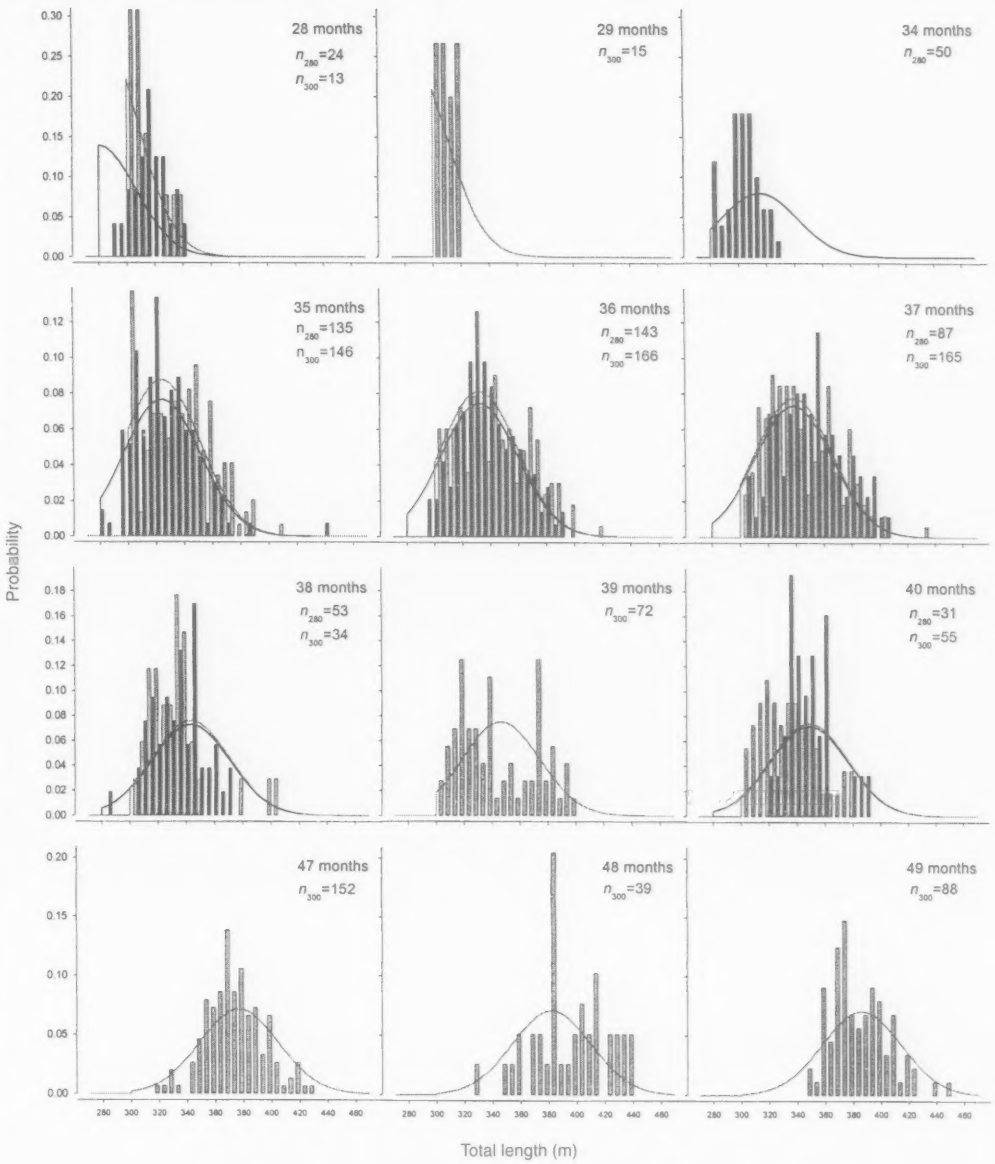

Figure 5

Female Gulf St. Vincent length-frequency histograms expressed as proportion of fish caught per 5-mm length class. Ages (by month) illustrated were those of largest sample size. Black bars correspond to fish caught when the fishery was subject to a 280-mm size limit, and gray bars for fish caught under a 300-mm size limit. The fitted normal likelihood probability density curves (Eq. 4) calculated for each size limit have been overlaid for comparison.

samples were obtained in the ages (~30 months) at which the faster fish are entering the legal-size stock. These clumps of points lie well above the estimated mean length at age. In the absence of the truncation method, the mean curves would pass through these points.

Only the Akamine-Richards model failed to converge with the South Australian King George whiting data sets. Because the Richards form of the model includes both the exponent and its inverse in different places in the formula, it is likely to result in a more numerically challenging

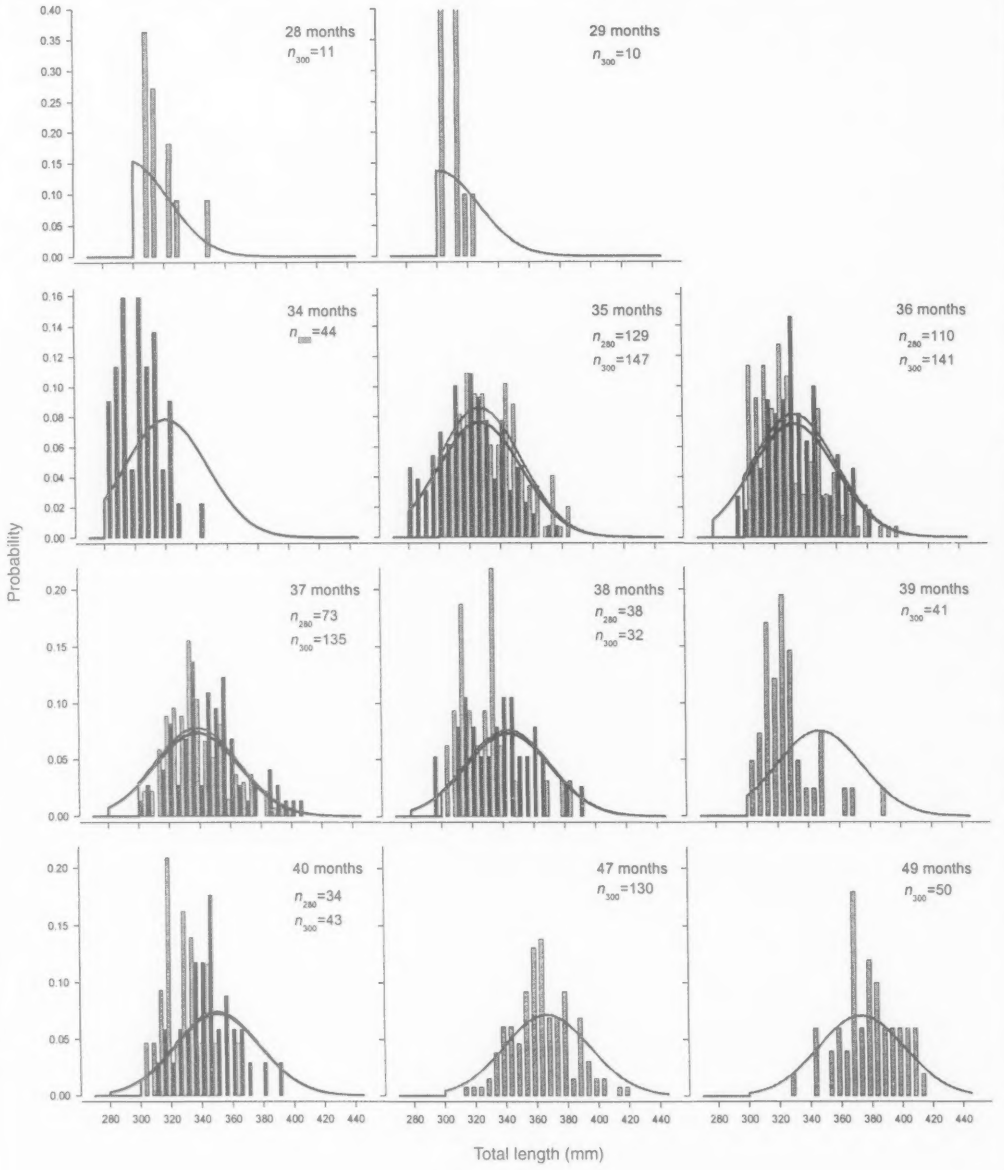

Figure 6

Male Gulf St. Vincent length-frequency histograms and fitted truncated normal density curves, as in Figure 5.

minimization algorithm. The two occurrences of the parameter, r, in the Richards formula $L = L_\infty/\{1 + re^{-K(t-t_0)}\}^{1/r}$, as a factor in front of the negative exponential and as its reciprocal exponent around the entire function apart from L_∞ can act in contrary fashion. For $r > 1$, increases in r imply an increase in length-at-age because of the parameter as a reciprocal exponent, and the opposite for the second role the parameter plays in describing mean length. We speculate that the Richards growth formula was less numerically robust because r can rise and fall at different parameter ranges along the path to convergence, resulting in a more complex likelihood surface.

Modeling the full length distribution at each monthly age is valuable for assessing populations of heavily ex-

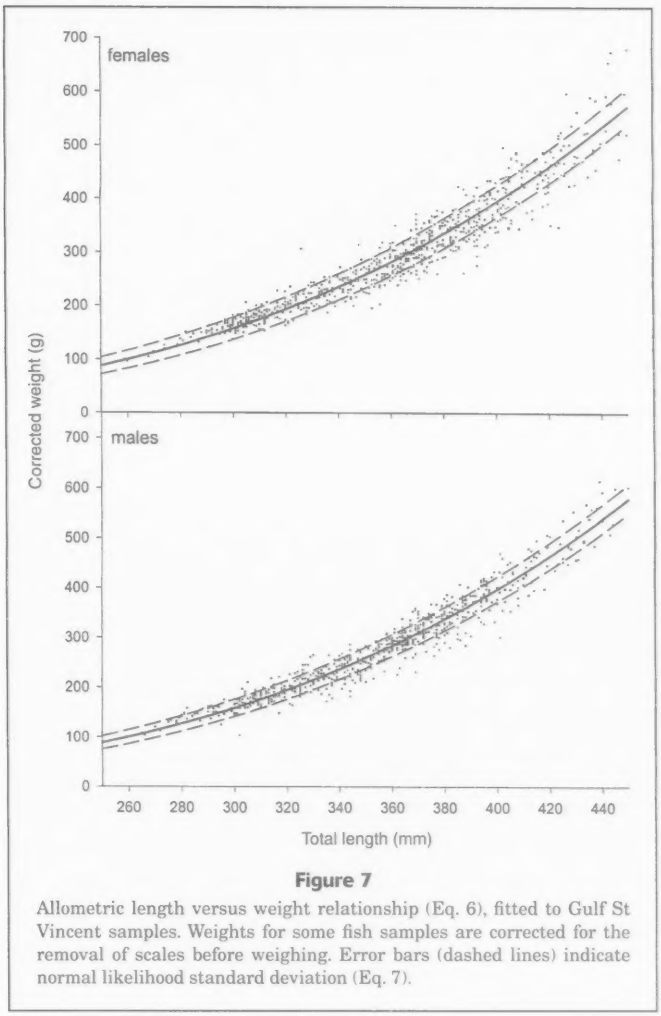

Figure 7

Allometric length versus weight relationship (Eq. 6), fitted to Gulf St Vincent samples. Weights for some fish samples are corrected for the removal of scales before weighing. Error bars (dashed lines) indicate normal likelihood standard deviation (Eq. 7).

ploited species such as King George whiting where depletion of the legal sizes of the cohort is rapid over monthly time scales. In fishery stock assessment models where only legal-size lengths of each yearly cohort are subject to exploitation and where size selection is driven primarily by a legal size limit rather than size-varying gear selectivity, model accuracy is improved by dividing the cohort length distribution into legal and sublegal components.

Growth was variable, reflected in high standard deviations in lengths-at-age of King George whiting. This meant a time span of 12–24 months between the crossing into legal size of the first (i.e. fastest growing, at ~23 months of age) and last 2% of the normal cohort to reach LML. Because fishing mortalities are such that a majority of fish are removed within 24 months of reaching legal size, the explicit representation of the distribution of harvestable lengths of cohorts as they cross LML allows substantial improvements in stock assessment, notably in fitting only legal sizes to monthly catch totals by weight and sampled numbers at age. Moreover, the seasonal variations in fishing effort targeted on South Australian King George whiting appear to track the arrival of the bulk of recruits to legal size in autumn and early winter. The growth model presented in our study allowed this feature of seasonal timing in recruitment to be captured in the associated stock assessment population model.

Acknowledgments

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Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska

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Abstract–We analyzed data from National Marine Fisheries Service bottom trawl surveys carried out triennially from 1984 to 1996 in the Gulf of Alaska (GOA). The continental shelf and upper slope (0–500 m) of the GOA support a rich demersal fish fauna dominated by arrowtooth flounder (*Atheresthes stomias*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), and Pacific Ocean perch (*Sebastes alutus*). Average catch per unit of effort (CPUE) of all groundfish species combined increased with depth and had a significant peak near the shelf break at 150–200 m. Species richness and diversity had significant peaks at 200–300 m. The western GOA was characterized by higher CPUEs and lower species richness and diversity than the eastern GOA. Highest CPUEs were observed in Shelikof Strait, along the shelf break and upper slope south of Kodiak Island, and on the banks and in the gullies northeast of Kodiak Island. Significant differences in total CPUE among surveys suggest a 40% increase in total groundfish biomass between 1984 and 1996. A multivariate analysis of the CPUE of 72 groundfish taxa revealed strong gradients in species composition with depth and from east to west, and a weak but significant trend in species composition over time. The trend over time was associated with increases in the frequency of occurrence and CPUE of at least eight taxa, including skates (Rajidae), capelin (*Mallotus villosus*), three flatfish species, and Pacific Ocean perch, and decreases in frequency of occurrence and CPUE of several sculpin (*Myoxocephalus* spp.) species. Results are discussed in terms of spatial and temporal patterns in productivity and in the context of their ecological and management implications.

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The continental shelf and upper slope of the Gulf of Alaska (GOA, Fig. 1) support a diverse community of demersal fishes. This community includes many commercial species that support rich bottom trawl and longline fisheries with landings averaging approximately 250,000 metric tons per year over the past two decades (NPFMC[1]). The commercially most important species during the past decade have been walleye pollock (*Theragra chalcogramma*), Pacific halibut (*Hippoglossus stenolepis*), Pacific cod (*Gadus macrocephalus*), other flatfish species (Pleuronectidae), rockfish (*Sebastes* spp.), and sablefish (*Anoplopoma fimbria*). Arrowtooth flounder (*Atheresthes stomias*), although currently the dominant demersal species by biomass, is a minor component of total landings.

Triennial bottom trawl surveys have been carried out since 1984 to assess the abundance and distribution of the main commercial species in the GOA (Martin, 1997). The surveys also provide data on noncommercial fish species and other associated benthic megafauna. At least 140 species of fishes belonging to 33 families were collected during the 1996 GOA bottom trawl survey (Martin, 1997). Rockfish (Scorpaenidae) were the best represented family with 25 species, followed by sculpins (Cottidae, 24 species) and flatfishes (Pleuronectidae, 16 species). Data from similar bottom trawl surveys have been used to investigate the ecology and zoogeography of fish assemblages in many parts of the world, including the North Pacific (Gabriel and Tyler, 1980; Rogers and Pikitch, 1992; Jay, 1996). However, to our knowledge there have been no studies in which demersal fish assemblages from the GOA shelf and slope were examined.

To understand, and eventually to predict, the effects of environmental variations on fish stocks, scientists and managers increasingly advocate ecosystem approaches to research and management (Yaffee et al., 1996; Langton and Haedrich, 1997). Ecosystem management must be based on multispecies relationships and overcome the current focus on individual species (Langton and Haedrich, 1997). An important prerequisite for successful multispecies approaches is an understanding of the species structure of fish communities in space and time.

The purpose of this paper is to identify spatial and temporal patterns in the composition of the demersal fish community from the GOA. Specific objectives are 1) to identify the main environmental and spatial gradients along which the groundfish community is structured, and 2) to identify long-term changes in the composition of the groundfish community.

[1] NPFMC (North Pacific Fisheries Management Council). 1997. Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska. North Pacific Fisheries Management Council, 605 West 4th Ave., Suite 306, Anchorage, AK 99501.

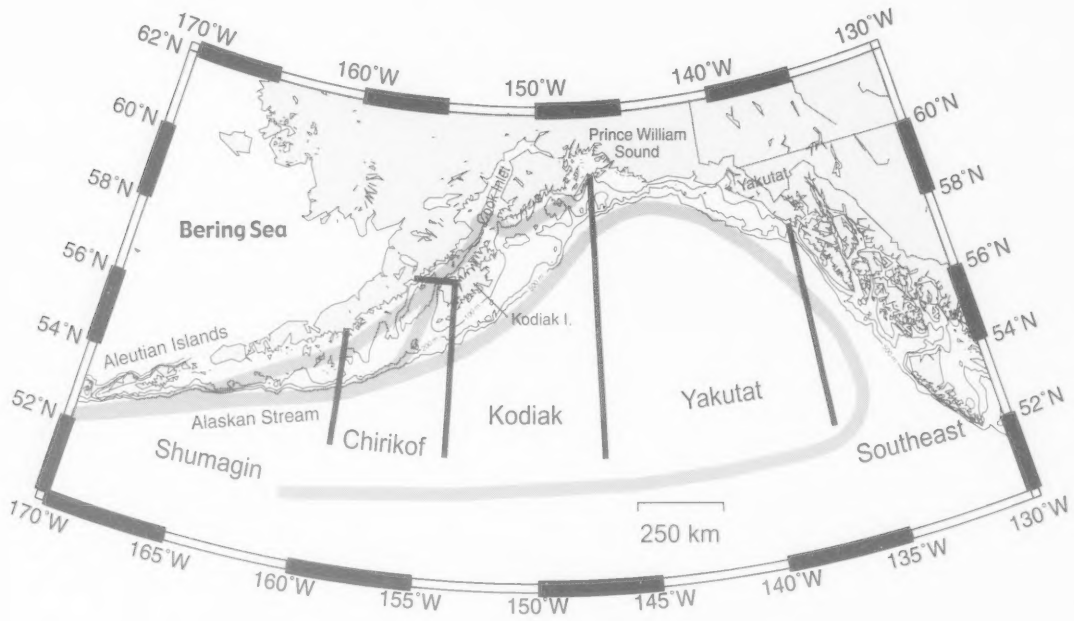

Figure 1

Bathymetric and geographic features of the Gulf of Alaska between 130°W and 170°W. The black vertical lines separate the five areas used in the survey design and analysis. Thin lines indicate 100 m, 200 m, and 500-m isobaths. The large shaded lines summarize major circulation patterns.

Materials and methods

Study area

Our study area included the continental shelf and the upper continental slope along the perimeter of the GOA to a depth of 500 m (Fig. 1). The total study area is approximately 300,000 km^2, extending over a distance of 2600 km from Southeast Alaska to the western Aleutian Islands.

Data sources

All fisheries data for this study were obtained from the Alaska Fisheries Science Center (AFSC), National Marine Fisheries Service (NMFS) in Seattle, WA. Personnel from AFSC have executed bottom trawl surveys of groundfish stocks in the GOA on a triennial basis since 1984 (Table 1). All surveys were conducted during the summer with chartered fishing vessels and were based on a stratified random sampling design. The GOA was divided into five areas, three in the western GOA (Shumagin, Chirikof, Kodiak) and two in the eastern GOA (Yakutat, Southeast, see Fig. 1) and four depth strata (0–100 m, 100–200 m, 200–300 m, 300–500 m). Depth strata within each area were further subdivided into 2–5 strata based on the type of geographical area (e.g. banks, gullies, shelf, and slope), resulting in a total of 49 strata. Some modifications were made to the stratification scheme after 1987. Our analysis was based on current stratum boundaries. Details of the sampling design, data collection, and sample processing are described in Brown (1986), Martin and Clausen (1995), Stark and Clausen (1995), and Martin (1997). In our analysis we excluded data from the 0–100 m stratum in the southeast area because it is mostly untrawlable and was not sampled during three out of five surveys; thus we used a total of 48 strata in the analysis. We further excluded all hauls that were classified as unsatisfactory in the database.

Several types of fishing gear were used in the bottom trawl surveys between 1984 and 1996. A poly-Nor'eastern high opening bottom trawl equipped with rubber bobbin roller gear has become the standard gear for GOA bottom trawl surveys (Munro and Hoff, 1995) and was used for at least part of the survey in all years (Table 1). In addition, an older Nor'eastern trawl (gear type 160) was used during parts of the 1984 and 1990 survey and two different Japanese trawls (Table 1) were used during the 1984 and 1987 joint Japanese-American surveys. Fishing effort for each gear type was spread out over most of the sampling region within each year and one gear type (gear type 172) was used during all surveys, allowing us to estimate gear differences.

Data analysis

Our analysis was based on standardized catch per unit of effort of 72 fish taxa collected in the bottom trawl surveys. Catches were standardized to weight per unit area (kg/km^2), where the area swept by the trawl was estimated

Table 1

Number of quantitative hauls used in analysis by gear type, start and ending dates of survey, minimum, maximum, and average depth of hauls, and number of haul locations for which bottom temperature was obtained. Note changes in gear from 1984 to 1990, which were associated with a decrease in the average tow duration. Gear types: 160 = Nor'eastern trawl; 172 = poly-Nor'eastern high opening bottom trawl; 710 = Japanese poly trawl; 717 = Japanese poly trawl with roller gear.

	1984	1987	1990	1993	1996
Total number of hauls	867	758	705	774	807
Gear type: no. of hauls	(160: 430) (172: 133) (710: 304)	(172: 380) (717: 378)	(160: 166) (172: 539)	(all: 172)	(all: 172)
Starting date	Jun 3	May 22	Jun 4	Jun 6	May 22
Ending date	Oct 2	Sep 10	Sep 9	Sep 7	Jul 30
Average depth (m)	167	150	167	156	157
Maximum depth (m)	499	499	494	488	479
Minimum depth (m)	16	20	20	22	20
Temp. measurements	563	298	285	726	716

from the measured distance trawled and estimates or measurements of the width of the net opening. Taxa to include in the analysis were selected according to the following criteria: 1) all species consistently identified to species level and occurring at least at 1% of the stations, 2) taxa that were not consistently identified to species level were combined by genus or, if necessary, by family, 3) if, after grouping taxa, a species, genus, or family was present at less than 1% of the stations within each year, it was not included in the analysis.

As an initial estimate of abundance trends, we computed gulf-wide averages of CPUE for each species by year. CPUEs from the Japanese trawls used in 1984 and 1987 were adjusted to the US standard trawl gear by using fishing power coefficients provided in Tables 28 and 31 in Munro and Hoff (1995). Following standard NMFS methods (Martin, 1997), we averaged estimated CPUEs by stratum, weighted the averages by stratum area, and combined them to obtain area-wide averages.

From a haul-by-taxon matrix of CPUE data, we computed univariate and multivariate indices to examine spatial and temporal patterns in community structure. For each haul we computed species richness (number of species), species diversity (Shannon-Wiener index), and total CPUE of all groundfish taxa combined as univariate measures of community structure. We considered three indices of species diversity (Shannon-Wiener, Simpson's D, Fisher's α) and chose the Shannon-Wiener index because it showed little dependence on sample size in simulations, was approximately normally distributed (which facilitates statistical comparisons), and is widely used in the ecological literature. In addition, we computed multivariate indices of species composition based on Bray-Curtis dissimilarities of root-root transformed CPUEs and nonmetric multidimensional scaling (NMDS) as described in Mueter and Norcross (1999). Indices of species composition were computed separately for each year and were related to explanatory variables to describe the major gradients in species composition by year. To examine trends in species composition over time, catches were averaged by stratum instead of using individual hauls, reducing the 3911 hauls to 240 within-year strata (5 years × 48 strata). An NMDS ordination of the stratum-by-species matrix was then used to test specifically for significant trends in species composition over time. We computed the linear combination of ordination axes that maximized the correlation with year and tested whether the correlation was significantly higher than would be expected by chance by using randomization tests. This linear combination was used as an index representing changes in species composition over time (time index). Species that were most strongly associated with the time index were identified based on scatterplots and Spearman rank correlations between the index and individual species abundances, and changes in these species were examined in more detail.

Depth, geographic location, bottom temperature (measured by sensors attached to the gear), Julian day, year, gear type, and area swept were included in the analysis as explanatory variables. Geographic location was represented in the analysis either as a categorical variable by using the five statistical areas depicted in Figure 1 or by using alongshore distances (AD). Alongshore distance was computed by projecting each station onto a line that approximately followed the shelf break and measuring the distance along this line from its origin in the southeast part of the study area (km 0) to the westernmost point (km 2600). Temperature was not measured for all hauls (Table 1); thus all regressions were done both with and without temperature included. Gear type was included in all models to account for potential differences among gear types. Area swept was only included for examining trends in species richness and diversity because the number of species per haul was expected to increase with the area sampled. All other indices were based on standardized CPUEs.

Generalized additive models (GAM, Hastie and Tibshirani, 1990) and linear models were used to relate univariate and multivariate indices, individual species CPUEs, and presence-absence data to the independent variables. Additive models were used to allow for nonlinear relationships between the dependent and independent variables. A GAM is a nonparametric regression that uses smooth functions of the independent variables in place of linear functions and allows different probability distributions for the data. We initially assumed that species richness followed a Poisson distribution (counts), that the Shannon-Wiener index, log-transformed CPUEs, and all indices of species composition followed a normal distribution, and that presence-absence data followed a binomial distribution. The dependent variables were then modeled as the sum of nonparametric functions (smoothing splines) of the hypothesized independent variables. If no evidence of nonlinearity was found, linear terms were substituted for the smoothing splines. Residuals from each regression model were examined for violations of the underlying assumptions (error distribution and homogeneity of variance) and for outliers. Specifically, we examined residuals graphically by means of histograms, quantile-quantile plots, and plots of residuals against time and against other covariates. We further conducted formal tests of goodness-of-fit of the residuals against the assumed error distributions after each model fit. Model fits were generally deemed adequate, unless noted otherwise in the results.

To identify and evaluate the significance of relationships between species composition and explanatory variables we first chose the most appropriate regression model, then quantified the contribution of each explanatory variable to the model fit. A stepwise procedure based on the Akaike information criterion (Hastie and Tibshirani, 1990) was used to select a subset of significant variables. As a measure of model fit we computed a pseudo-coefficient of determination (pseudo-r^2), or the fraction of the total deviance explained by the model, as a surrogate for the familiar r^2 (Swartzman et al., 1992). The importance of individual variables in the model fits was evaluated similarly by using a pseudo-coefficient of partial determination based on reduced models that exclude the variable of interest (= 1 – deviance of best model/deviance of reduced model).

Trends in the abundance of those species that were strongly associated with the time index were examined in greater detail by haul. For this analysis we treated zero and nonzero catches separately to test for 1) changes in the catch rate of a species over time based on positive catches only (CPUE-where-present) and 2) changes in the frequency of occurrence of a species over time (by estimating the probability of a nonzero haul). To test for changes in the CPUE-where-present of these species, we used an analysis of covariance model of the following form:

$$\log(CPUE\text{-}where\text{-}present) = area + depth\ stratum + gear + (area \times depth\ stratum) + \beta \times year.$$

Errors were assumed to be normally distributed, thus CPUE-where-present was assumed to follow a lognormal distribution. A separate linear time trend was estimated and evaluated for significance within each depth stratum in each area (β parameters). The interaction term (*area* × *depth stratum*) was omitted if it was not significant at the 5% level. Strata within the same statistical area and depth stratum were pooled, unless fitting separate regression lines to each of the 48 strata improved the overall fit significantly. If the slope of the regression did not differ among areas or depth strata at the 5% level, data were further pooled across areas or depth strata (or both) to obtain the most parsimonious model.

The probability of nonzero hauls was estimated similarly using a logistic regression model (McCullagh and Nelder, 1989):

$$\log\left(\frac{\Pr(CPUE>0)}{1-\Pr(CPUE>0)}\right) = area + depth\ stratum + gear + (area \times depth\ stratum) + \beta \times year,$$

where the number of positive catches (CPUE>0) was assumed to follow a binomial distribution. The most parsimonious models for each species were used to test the null hypothesis that there was no significant (linear) trend in the catch rate (CPUE-where-present) or frequency of occurrence (Pr(CPUE>0)) over time. The null hypothesis was rejected if the slope β was significantly different from zero at the 5% level.

Results

Arrowtooth flounder had the highest average CPUE (kg/km^2) and the highest frequency of occurrence during all surveys (Table 2). Walleye pollock was second in most years, followed by Pacific cod and Pacific halibut. However, in 1996, the estimated CPUE of Pacific Ocean perch exceeded that of pollock, cod, and halibut. Sablefish, five other flatfish species, two *Sebastes* species, and Atka mackerel (*Pleurogrammus monopterygius*) were other important species by CPUE (> 200 kg/km^2, Table 2). The most abundant species, including gadids and most of the flatfishes, were generally also the most widespread species in the survey (>50% frequency of occurrence). In spite of relatively high CPUEs, rockfishes, Atka mackerel, and yellowfin sole (*Limanda aspera*) had low frequencies of occurrence (4–40%), indicating high local abundances and a more restricted spatial distribution.

Independent variables used in the analysis of species richness, diversity, CPUE, and species composition were moderately correlated (Table 3). The largest correlations were between area swept and year (–0.452), due to a reduction in haul duration after 1987, between depth and temperature (–0.407), and between Julian day and alongshore distance (–0.383). Depth and bottom temperature on the shelf and slope are invariably confounded and their effects may generally be difficult to separate. The confounding between Julian day and AD was extreme in some years (e.g. r=–0.79 in 1993) because sampling vessels traveled from west to east during most surveys. However

Table 2

All groundfish taxa included in analysis and their estimated average CPUE (kg/km^2) by year and for all years combined. CPUEs were computed for each haul, averaged by stratum, weighted by stratum area, and combined to obtain area-wide averages. FO denotes overall frequency of occurrence for all years combined in percent.

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
Atheresthes stomias [1]	arrowtooth flounder	3790	3339	6499	5298	5574	4900	91
Theragra chalcogramma [1]	walleye pollock	2431	3139	2873	2586	2320	2670	74
Gadus macrocephalus [1]	Pacific cod	1876	1516	1424	1397	1821	1607	73
Hippoglossus stenolepis [1]	Pacific halibut	1415	1410	1118	2007	1936	1577	77
Sebastes alutus [1]	Pacific Ocean perch	753	823	535	1649	2629	1278	40
Anoplopoma fimbria [1]	sablefish	753	1379	731	844	492	840	52
Hippoglossoides elassodon [1]	flathead sole	912	783	828	643	689	771	57
Lepidopsetta spp. [1]	rock sole	515	668	531	590	695	600	44
Sebastes polyspinis [1]	northern rockfish	135	475	365	356	337	334	20
Pleurogrammus monopterygius	Atka mackerel	153	98	101	73	1179	321	5
Glyptocephalus zachirus [1]	rex sole	187	269	335	297	245	266	67
Microstomus pacificus [1]	Dover sole	164	263	329	291	266	263	55
Limanda aspera [1]	yellowfin sole	313	192	196	277	162	228	7
Sebastes ciliatus [1]	dusky rockfish	87	505	91	194	255	227	20
Sebastes aleutianus [1]	rougheye rockfish	153	227	165	212	156	183	34
Rajidae unident.	skate (unidentified)	139	129	164	205	274	182	33
Clupea pallasi	Pacific herring	186	511	60	53	3	163	8
Sebastes zacentrus	sharpchin rockfish	23	274	131	81	220	146	10
Albatrossia pectoralis	giant grenadier	115	96	81	155	175	124	3
Sebastolobus alascanus	shortspine thornyhead	126	127	68	114	177	122	24
Sebastes variegatus	harlequin rockfish	9	247	60	32	68	83	11
Thaleichthys pacificus	eulachon	24	56	95	119	110	81	32
Isopsetta isolepis [1]	butter sole	80	71	59	102	71	77	7
Platichthys stellatus [1]	starry flounder	50	63	35	137	93	76	5
Sebastes borealis	shortraker rockfish	59	137	43	69	69	75	8
Sebastes proriger	redstripe rockfish	18	90	92	101	51	71	4
Squalus acanthias	spiny dogfish	34	34	65	114	96	69	16
Hemilepidotus jordani	yellow Irish lord	49	46	40	40	61	47	27
Sebastes brevispinis	silvergray rockfish	16	18	48	65	82	46	7
Ophiodon elongatus	lingcod	15	32	35	53	80	43	10
Hemitripterus bolini	bigmouth sculpin	54	35	29	19	14	30	18
Lamna ditropis	salmon shark	27	43	42	26	11	30	1
Myoxocephalus spp.	sculpin (unidentified)	37	23	18	22	30	26	9
Parophrys vetulus [1]	English sole	11	28	26	28	15	22	7
Somniosus pacificus	Pacific sleeper shark	1	1	6	29	72	22	1
Zaprora silenus	prowfish	13	24	15	28	23	21	11
Pleuronectes quadrituberculatus [1]	Alaska plaice	7	16	20	9	17	14	4
Microgadus proximus	Pacific tomcod	5.03	34.67	6.32	9.01	5.78	12.16	2
Sebastes babcocki	redbanded rockfish	4.88	6.21	11.20	12.53	15.54	10.07	11
Hydrolagus colliei	spotted ratfish	13.06	8.16	6.32	7.08	12.65	9.45	6
Hexagrammos decagrammus	kelp greenling	3.89	8.17	13.87	8.21	6.69	8.16	8
Sebastes reedi	yellowmouth rockfish	1.69	0.89	6.39	12.14	3.15	4.85	1
Sebastes ruberrimus	yelloweye rockfish	2.10	10.17	3.29	3.88	3.70	4.63	3
Sebastes helvomaculatus	rosethorn rockfish	1.99	5.12	2.50	2.54	7.71	3.97	4
Sebastes melanops	black rockfish	1.14	3.75	4.65	0.86	7.89	3.66	1
Bathymaster signatus	searcher	2.08	2.05	5.39	3.04	4.38	3.39	15
Trichodon trichodon	Pacific sandfish	7.56	3.71	2.45	1.76	0.52	3.20	3
Malacocottus spp.	sculpin (unidentified)	4.33	2.97	2.40	3.55	1.63	2.97	14
Cryptacanthodes giganteus	giant wrymouth	0.76	3.26	3.98	1.17	2.77	2.39	1
Lycodes palearis	wattled eelpout	0.86	1.75	3.10	3.16	2.30	2.23	11

continued

Table 2 (continued)

Scientific name	Common name	1984	1987	1990	1993	1996	Mean	FO
Eopsetta jordani	petrale sole	0.97	0.83	0.61	2.77	3.68	1.77	2
Mallotus villosus	capelin	1.47	0.17	0.51	0.42	4.98	1.51	7
Lycodes brevipes	shortfin eelpout	0.13	0.84	0.79	2.41	2.17	1.27	8
Dasycottus setiger	spinyhead sculpin	1.33	0.49	0.89	1.88	0.83	1.08	11
Aptocyclus ventricosus	smooth lumpsucker	0.74	1.29	1.77	0.37	0.56	0.95	2
Podothecus acipenserinus	sturgeon poacher	0.19	0.42	1.23	2.34	0.33	0.90	5
Sebastes elongatus	greenstriped rockfish	0.05	0.22	0.59	0.91	1.20	0.59	1
Sebastes wilsoni	pygmy rockfish	0.00	1.38	0.30	0.01	0.96	0.53	1
Myctophidae	lanternfish (unidentified)	0.19	0.19	0.11	1.52	0.53	0.51	4
Triglops spp.	sculpin (unidentified)	0.37	0.32	0.68	0.40	0.61	0.48	6
Stichaeidae	prickleback (unidentified)	0.58	0.05	0.51	0.70	0.41	0.45	4
Sebastes crameri	darkblotched rockfish	0.02	0.13	0.59	0.99	0.41	0.43	1
Hexagrammos stelleri	whitespotted greenling	0.17	0.56	0.64	0.33	0.27	0.39	1
Lyopsetta exilis	slender sole	0.10	0.07	0.29	0.77	0.59	0.37	5
Cyclopteridae (Liparidinae)	snailfish	0.30	0.23	0.30	0.28	0.04	0.23	3
Hemilepidotus hemilepidotus	red Irish lord	0.07	0.29	0.05	0.32	0.10	0.16	1
Cottidae	sculpin (unidentified)	0.25	0.00	0.28	0.08	0.01	0.12	1
Gymnocanthus spp.	sculpin (unidentified)	0.16	0.03	0.00	0.06	0.06	0.06	1
Eumicrotremus orbis	Pacific spiny lumpsucker	0.02	0.08	0.03	0.07	0.04	0.05	2
Lycodes diapterus	black eelpout	0.08	0.05	0.00	0.01	0.02	0.03	2
Sarritor frenatus	sawback poacher	0.03	0.03	0.01	0.04	0.04	0.03	2
Bathyagonus nigripinnis	blackfin poacher	0.02	0.01	0.01	0.01	0.00	0.01	1
Total		14,786	17,286	17,436	18,400	20,662	17,714	

[1] Catches for 1984 and 1987 were adjusted by using fishing power coefficients in Tables 28 and 31 in Munro and Hoff (1995). Other flatfishes were adjusted by using rock sole coefficients.

Table 3

Pairwise Pearson's correlation coefficients among independent variables used in the statistical analysis.

	Depth	Alongshore distance	Gear temperature	Julian day	Year
Alongshore distance	–0.326*				
Gear temperature	–0.407*	–0.203*			
Julian day	0.129*	–.383*	0.330*		
Year	–0.026	–0.035	–0.266*	–0.306*	
Area swept	0.012	0.184*	0.019	0.145*	–0.452*

* Highly significant (P=0.01)

the direction of sampling was reversed in some years, providing some contrast.

Species richness, as measured by the number of species per haul, was initially modeled as a Poisson variable (counts). However, an analysis of the distribution of the observed numbers and of residuals from the fitted models suggested that it could more appropriately be modeled as a normally distributed variable (see below). We fitted models assuming either a Poisson or a normal distribution and found that the estimated patterns were virtually identical and in both cases the same model was selected as best model. Only results based on the normal distribution are presented. Species richness was highly variable and the best model explained a small portion of the overall variability (Pseudo-r^2=0.25). The average number of species increased with area swept (Fig. 2), which may be expected if species area relationships established for terrestrial ecosystems also hold in the marine environment. The number of species tended to peak at intermediate depths (200–300 m) and was highest in the eastern GOA (Table 4), decreasing steadily west of Prince William Sound (km 1100, approximately 147°W). Species richness appeared

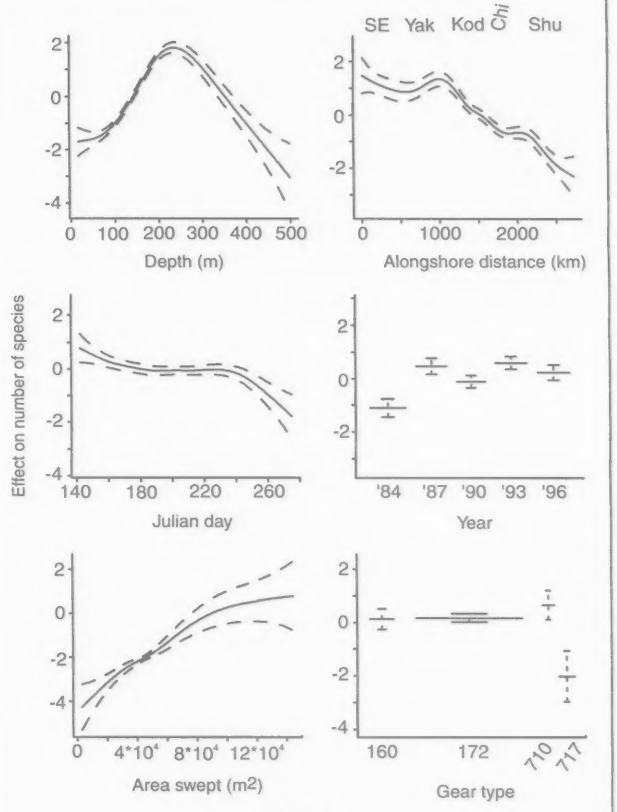

Figure 2

Estimated trends in number of species per haul by depth, alongshore distance, Julian day, year, area swept, and gear type. Alongshore distance was measured along the 200-m depth contour from east to west. Major geographic regions from east to west are Southeast (SE), Yakutat (Yak), Kodiak (Kod), Chirikof (Chi), and Shumagin (Shu). Dashed lines indicate approximate 95% confidence limits of the regression lines. Horizontal lines in lower right plots indicate mean response with 95% pointwise confidence intervals. Width of bars is proportional to number of observations. Fitted lines in each panel are adjusted for the effects of all other variables. Standardized effects in each plot (y-axes, no units) are on the same scale for comparison. Effects are standardized because the estimated CPUE at a given value of a variable is dependent upon the levels of all other variables.

to decrease during the last month of the survey season and showed some variation across years (Fig. 2). There was no consistent trend in species richness with temperature (not shown). One of the Japanese trawls (gear type 717, Fig. 2) tended to have a much smaller number of species per haul on average, suggesting a low catchability for at least some species. Residuals from the best model were close to normally distributed (Fig. 3, A and B) and showed no apparent trends with any of the covariates or over time.

Only a very small portion of the variability in species diversity (Shannon-Wiener index) was accounted for by the best regression (Pseudo-r^2=0.17). Depth had the strongest effect on species diversity with highest diversities observed at intermediate depths (Fig. 4). Diversity generally increased with the number of species, which showed a very similar trend with depth (Fig. 2). Diversity was higher in the eastern Gulf and decreased west of Prince William Sound (Figs. 4 and 5). It showed little variation over time, both within the survey period and across years. However,

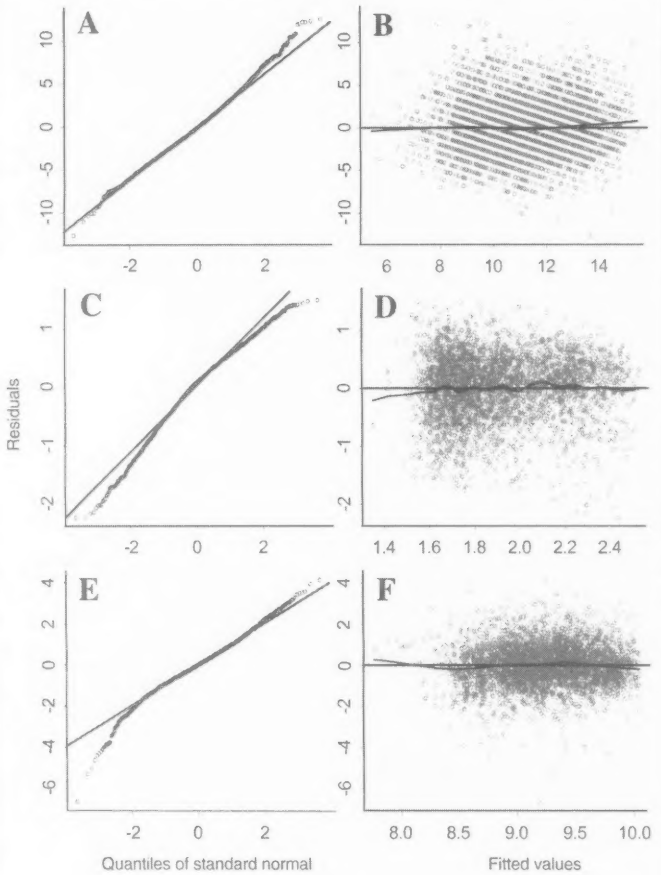

Figure 3

Quantile-quantile plots (left), showing sorted residuals (points) against corresponding quantiles of the standard normal distribution, and plots of residuals against fitted values with smoothing spline (right) for best-fit models of species richness (**A**, **B**), species diversity (**C**, **D**), and total CPUE (**E**, **F**). Points in Q-Q plots fall on the indicated straight line if data are normally distributed.

Table 4

Average number of groundfish species caught per haul by depth stratum and geographic area, not adjusted for effects of other variables.

Depth stratum (m)	No. of species/haul (SE)	Area	No. of species /haul (SE)
0–100	9.5 (0.12)	Shumagin	9.7 (0.11)
100–200	11.5 (0.08)	Chirikof	10.5 (0.12)
200–300	13.2 (0.13)	Kodiak	11.6 (0.11)
300–500	10.9 (0.15)	Yakutat	12.5 (0.14)
		Southeast	12.8 (0.20)

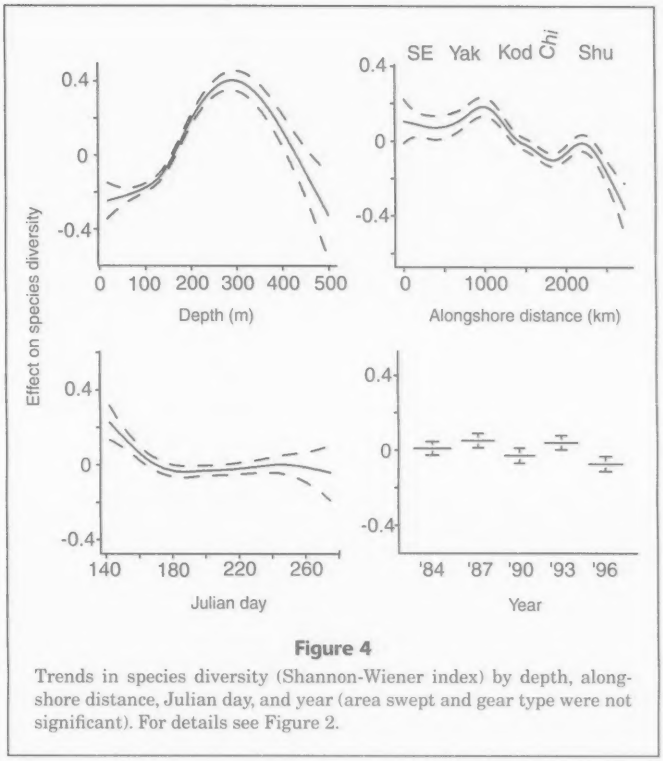

Figure 4

Trends in species diversity (Shannon-Wiener index) by depth, alongshore distance, Julian day, and year (area swept and gear type were not significant). For details see Figure 2.

95% confidence intervals suggest a significant drop in species diversity between 1993 and 1996. Area swept and temperature did not enter the best model, suggesting they had no strong effect on species diversity. Diagnostic plots indicated approximate normality and no apparent trends in the residuals (Fig. 3, C and D).

Total biomass (CPUE) showed strong trends with depth and alongshore distance (Fig. 6) but had high variability around these trends (Pseudo-r^2=0.14). Average CPUE increased sharply with depth to about 150 m—a trend that reflected, on average, approximately a doubling of CPUE between the shallowest sampling stations and stations at 150–200 m depth. A similarly strong gradient exists in the alongshore direction between Yakutat (km 700) and the Kodiak Island area (km 1500), where total CPUE has a pronounced maximum. Estimates of the spatial trend suggested that highest CPUEs are found around Kodiak Island, particularly in Shelikof Strait, along the shelf break and upper slope, and on the banks and in the gullies northeast of Kodiak Island (Fig. 5). Total CPUE appeared to decrease significantly after approximately Julian day 240 (Aug. 28); however, Julian day was confounded with alongshore distance (r =–0.38, Table 3) and the effect could in part be due to lower abundance in the eastern GOA, which was often sampled later than other areas. Gear effects were significant and indicated a lower catch rate for one of the Japanese trawls (gear 717, Fig. 6). The estimated time trend (Fig. 6) indicated a significant increase in total CPUE between 1984 and 1996 (P<0.001), based on a chi-square test of the difference in residual deviances (Hastie and Tibshirani, 1990). We estimated that the combined CPUE of all groundfish species included in the analysis increased from a gulf-wide average of 14,786 kg/km^2 in 1984 to 20,600 kg/km^2 in 1996 (Table 2), representing an increase of 40%. No significant effect of temperature on total CPUE was found. Diagnostic plots indicated approximate normality and no apparent trends in the residuals (Fig. 3, E and F).

The biomass of 72 groundfish species in 240 stratum/year combinations could effectively be summarized by an NMDS ordination in three dimensions (stress=0.085). Our findings suggested that the main gradients along which species composition varied were depth and alongshore distance, whereas temperature and temporal gradients (within and between years) had relatively minor effects on these indices of species composition. The first two dimensions (axes 1 and 2) of the ordination accounted for 67% and 19% of the overall variation respectively. An ordination plot of the first two axes indicated that the sample strata were most clearly separated along the depth gradient (Fig. 7). The alongshore gradient was roughly perpendicular to the depth gradient and clearly distinguished areas Southeast from the other areas (Fig. 7). Yakutat strata occupy an intermediate position between the Southeast strata and strata in other areas. Kodiak, Chiniak, and Shumagin were similar in species composition, as sug-

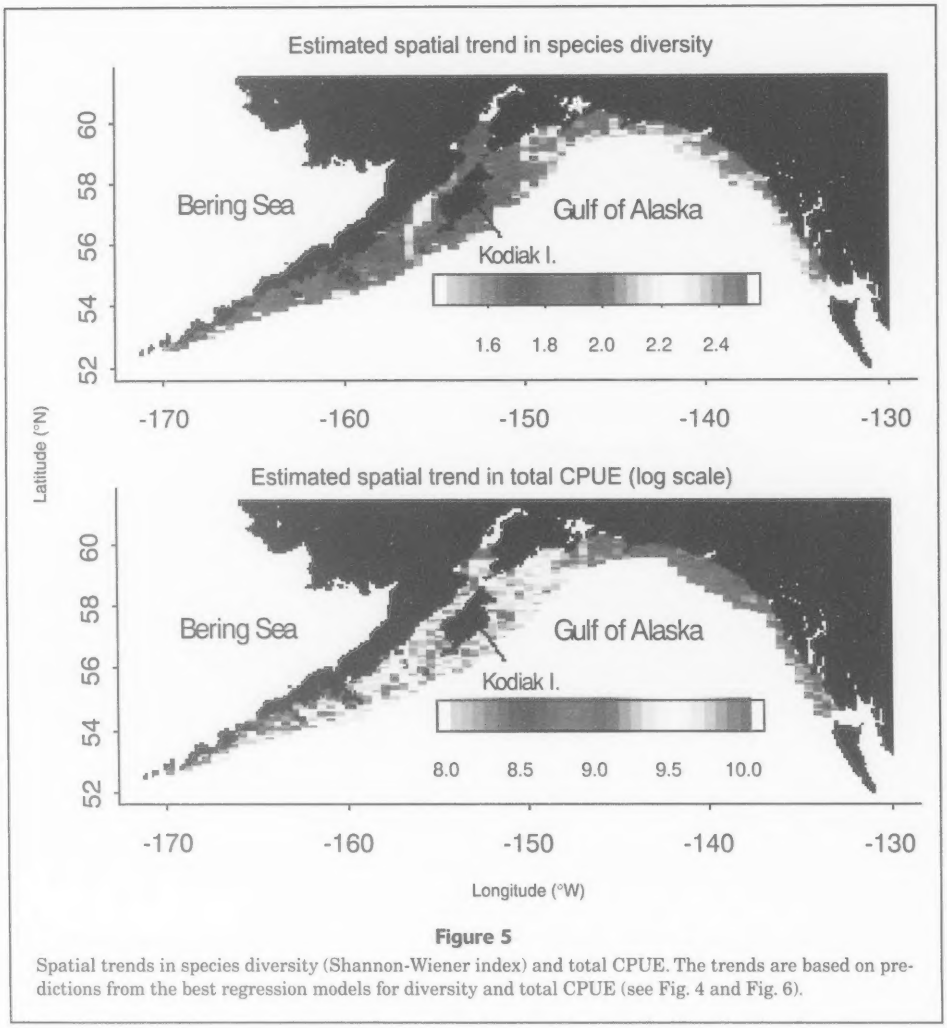

Figure 5

Spatial trends in species diversity (Shannon-Wiener index) and total CPUE. The trends are based on predictions from the best regression models for diversity and total CPUE (see Fig. 4 and Fig. 6).

gested by a substantial overlap in the location of strata in the ordination diagram. A three-way analysis of variance for each of the three axes by depth stratum, area, and year indicated highly significant differences for all three axes between depth strata and geographic areas, but weak and nonsignificant differences among years (Table 5), suggesting a relatively stable species composition from 1984 to 1996. Residuals from the ANOVA for axis 1 and 3 were approximately normally distributed and showed no apparent violations of the ANOVA assumptions. Residuals for axis 2 had a very long-tailed distribution, but an analysis of variance based on ranks yielded very similar results; therefore the conclusions appear to be robust.

Ordinations of individual hauls within each year confirmed that depth and alongshore distance explained much of the variation in species composition within years. The species composition in each year was effectively summarized by ordinations in five dimensions with Kruskal's stress values that were very close to 0.1 in all years (axes 1–5 in Table 6). The first axis of all five ordinations accounted for 42–47% of the variation in species composition. This axis, as well as most of the other axes, was most strongly related to the depth gradient in all years (Table 6). Alongshore distance appeared to explain a relatively small proportion of the variance in species composition. However the pseudo-coefficients of partial determination for alongshore distance typically increased substantially if Julian day was excluded from the model because of high correlations between Julian day and alongshore distances. Regressions of the axes on depth and alongshore distance alone resulted in pseudo-r^2 values that were very close to those from models that included Julian day. Furthermore, residuals from these models were not significantly related to Julian day for any year ($P>0.5$) based on linear regres-

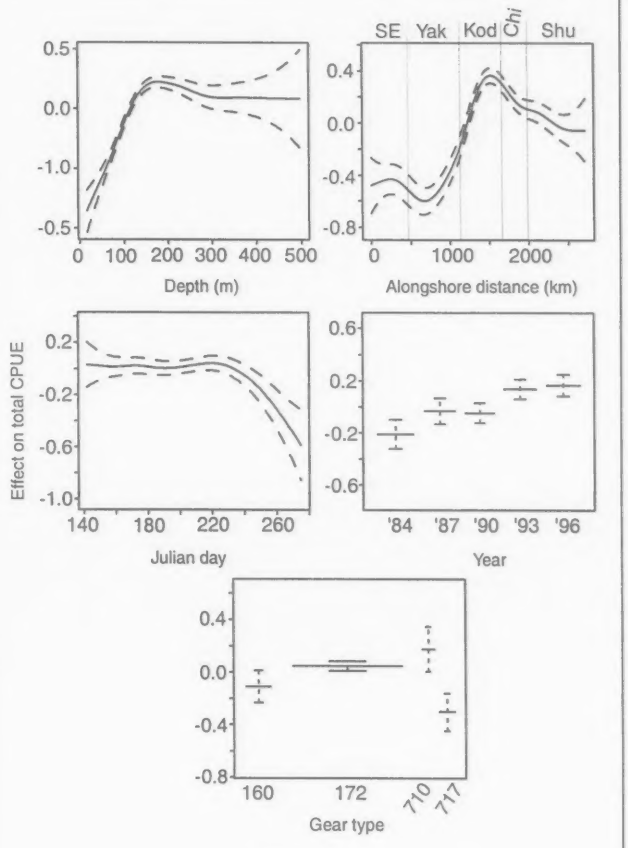

Figure 6

Trends in total CPUE by depth, alongshore distance, Julian day, year, and gear type. For details see Figure 2

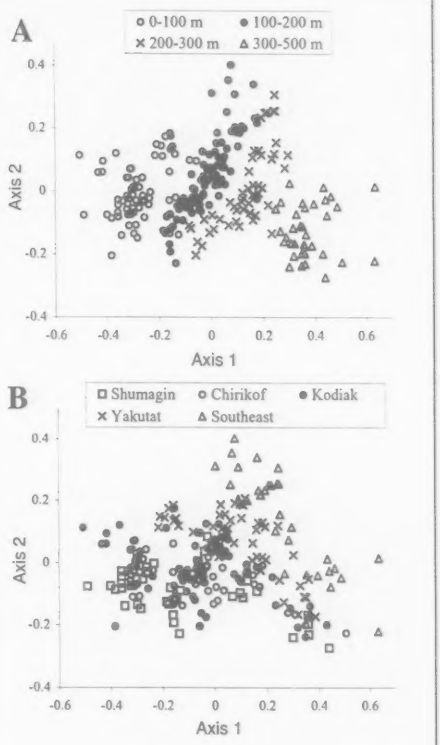

Figure 7

Plots of the first two axes from an NMDS (multidimensional scaling) ordination of 48 strata sampled during each of fivfe years. Distances between two points (strata) in the ordination diagram approximately reflect their dissimilarity in terms of species composition. Symbols indicate depth strata (**A**) and geographic area (**B**).

sions). These findings suggest that species composition within the summer remains relatively stable over the 14–16 week survey period.

To examine effects of temperature on species composition we used only those hauls from the 1993 and 1996 data for which temperature measurements were available (n=726 and n=716 respectively, Table 1). Results for other years are not reported because of the relatively small number of temperature measurements. The available temperature data for earlier years were often localized in certain strata, whereas large areas had few if any measurements. The lack of contrast did not allow definite conclusions with regards to the temperature effect. For 1993 and 1996, we repeated the GAM analysis for the five axes of species composition with temperature included. Temperature effects were apparently large. However, wide confidence intervals and inconsistent patterns between years suggest that the apparent effects were at least in part due to confounding of temperature with alongshore distance and depth. Therefore we first adjusted for the effects of depth and alongshore distance using the regression models summarized in Table 6. Temperature explained a small but significant portion of the remaining residual variation in three of the ordination axes in both 1993 and 1996 (Pseudo-r^2 values <0.1).

To identify which species were most strongly related to the major gradients we computed rank correlations between each species and the three axes of species composition based on the NMDS ordination of strata averages. We considered all species that had a positive or negative rank correlation of at least 0.4 with one of the axes for further examination, based on a visual inspection of scatterplots. Species associated with the first two axes were clearly separated along gradients of depth and alongshore distance (Figs. 8 and 9). The first axis was positively correlated with a number of deep-water species that were

Table 5

Analysis of variance of three axes of species composition by statistical area, depth stratum, and year.

Effect	df	Sum of squares	Mean squares	*F*-value	*P*-value
Axis 1					
Depth stratum	3	129.793	43.264	613.856	0.000
Area	4	10.350	2.588	36.713	0.000
Year	4	0.665	0.166	2.358	0.056
Depth stratum:area	11	1.756	0.160	2.265	0.014
Depth stratum:year	12	0.412	0.034	0.487	0.920
Area:year	16	0.291	0.018	0.258	0.998
Depth stratum:area:year	44	0.839	0.019	0.271	1.000
Residuals	145	10.220	0.070		
Axis 2					
Depth stratum	3	6.601	2.200	37.581	0.000
Area	4	27.771	6.943	118.587	0.000
Year	4	0.346	0.087	1.478	0.212
Depth stratum:area	11	1.091	0.099	1.694	0.080
Depth stratum:year	12	0.366	0.030	0.521	0.899
Area:year	16	1.017	0.064	1.086	0.374
Depth stratum:area:year	44	0.815	0.019	0.317	1.000
Residuals	145	8.489	0.059		
Axis 3					
Depth stratum	3	0.478	0.159	1.231	0.301
Area	4	9.541	2.385	18.423	0.000
Year	4	0.615	0.154	1.188	0.318
Depth stratum:area	11	3.080	0.280	2.163	0.019
Depth stratum:year	12	0.212	0.018	0.137	1.000
Area:year	16	0.698	0.044	0.337	0.992
Depth stratum:area:year	44	1.365	0.031	0.240	1.000
Residuals	145	18.773	0.129		

more abundant in the eastern GOA, but generally had a broad geographic distribution. The deep-water species included several rockfish species, rex sole (*Glyptocephalus zachirus*), Dover sole (*Microstomus pacificus*), sablefish, and myctophids. The alongshore distribution of CPUE suggests that many species displayed local maxima in biomass on the scale of 100–200 km (Fig. 8). The first axis was negatively correlated with a group of shallow-water species that were typically more abundant in the western GOA. The shallow-water group included a number of flatfish species, gadids, and sculpins. Many of the shallow water species had pronounced peaks in biomass at the longitude of Kodiak Island (km 1400–1700) and between the Shumagin Islands and Sanak Island (km 2000–2200).

The second axis was positively correlated with a "shelf break" group. Most of the species in this group had a pronounced peak in biomass near 200 m and were found primarily in the eastern GOA (Fig. 9). The group included a number of rockfish species, as well as lingcod (*Ophiodon elongatus*), petrale sole (*Eopsetta jordani*), and slender sole (*Lyopsetta exilis*). Species that were negatively or positively associated with the third axis (not shown) were not differentiated along gradients of depth and alongshore distance, suggesting that the third axis, which accounted for 14% of the overall variation, was related to other, unidentified gradients.

Finally, we examined trends in species composition over the 12-year period from the first survey in 1984 to the most recent survey in 1996 in more detail based on the NMDS ordination of species CPUEs averaged by stratum (Fig. 7). Although the individual indices of species composition were not significantly different among years (Table 5), a canonical correlation between the ordination axes and time (survey years) indicated a highly significant trend ($P<0.001$) in species composition. The linear combination of ordination axes that maximized the correlation with survey year was used as an index for the trend in species composition ("time index"). The index increased in most areas and depth strata between 1984 and 1996. Eight species that were positively correlated with the time index showed significant and increasing trends in either CPUE-where-present or frequency of occurrence for at least two area-depth stratum combinations (Fig. 10). Skates were most strongly associated with the index and showed a widespread increase in CPUE-where-present and frequency of occurrence, particularly in the Chirikof,

Table 6

Results from NMDS (multidimensional scaling) ordinations of species CPUEs in five dimensions (axes 1–5) by year, and GAM (generalized additive models) results for regressions of axis scores on depth, alongshore distance, and Julian day. Variance indicates proportion of overall variation accounted for by each axis. Stress indicates Kruskal's stress values for each ordination. Numbers for the full model indicate pseudo-r^2 values for the best model fit (1 – deviance of the best fitting model/deviance of the null model). Numbers following individual variables indicate pseudo-coefficient of partial determination, computed from a reduced model that excluded the variable (= 1 – deviance of best model / deviance of reduced model). Only coefficients of determination exceeding 0.1 are shown. Coefficient of determination for Julian day did not exceed 0.1 in any year or for any axis. AD = alongshore distances.

Year		Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Stress
1984	Variance	44%	19%	14%	12%	11%	0.102
	Full model	0.84	0.28	0.26	0.58	0.13	
	Depth	0.74		0.19	0.42		
	AD	0.12	0.13		0.12		
1987	Variance	42%	22%	14%	12%	10%	0.100
	Full model	0.77	0.22	0.32	0.36	0.21	
	Depth	0.67	0.11	0.28	0.19	0.17	
	AD	0.15			0.24		
1990	Variance	42%	21%	15%	12%	10%	0.096
	Full model	0.83	0.37	0.29	0.34	0.16	
	Depth	0.69	0.23	0.17	0.27	0.10	
	AD	0.11	0.12	0.17			
1993	Variance	47%	18%	13%	11%	11%	0.098
	Full model	0.81	0.24	0.37	0.49	0.31	
	Depth	0.71		0.26	0.42	0.27	
	AD				0.21		
1996	Variance	44%	20%	14%	12%	10%	0.099
	Full model	0.78	0.22	0.31	0.55	0.34	
	Depth	0.71	0.11	0.18	0.40	0.17	

Kodiak, and Yakutat areas (Figs. 10 and 11). Another elasmobranch (Pacific sleeper shark, *Somniosus pacificus*), two osmerids (capelin, *Mallotus villosus*, and eulachon, *Thaleichthys pacificus*), three flatfish species (Dover sole, rex sole, and arrowtooth flounder), and one rockfish species (Pacific Ocean perch, *Sebastes alutus*) increased significantly in one or more areas and depth strata (Fig. 10). The frequency of occurrence of capelin in the trawl survey increased significantly, whereas CPUE-where-present did not change or, in some cases, decreased significantly. Closer examination revealed that the increase in frequency of occurrence occurred primarily between 1993 and 1996 (Fig. 12). Capelin were caught in 14% of all hauls in 1996, compared to only 7% in 1993. Changes in the CPUE-where-present of three flatfish species differed among species. Although Dover sole increased primarily in the eastern GOA (Yakutat and Southeast), rex sole increased most strongly in the Chirikof area (Fig. 10). In contrast, arrowtooth flounder increased in all areas, but only in the 0–100 m depth stratum. Although all three flatfish species increased significantly over time, estimates of their gulf-wide average CPUEs were highest in 1990 and declined from 1990 to 1996 (Table 2). Both the frequency of occurrence and CPUE-where-present of Pacific Ocean perch increased strongly in the Chirikof area, and frequency of occurrence decreased in the Yakutat area.

CPUE-where-present of the four species that were negatively correlated with the time index did not decrease significantly, and, in the case of rock sole (*Lepidopsetta* spp.), even increased in some areas (Fig. 13). However, frequency of occurrence decreased significantly for three of the species, particularly for bigmouth sculpin (*Hemitripterus bolini*, Fig. 13).

Discussion

Research survey data provide standardized indices of relative abundance that often track abundance trends more accurately than methods that use commercial catch data (Pennington and Stromme, 1998). However, results need to be interpreted with caution because the catchability of species may change over time owing to changes in survey gear, vessel type, spatial distribution, or the length composition of a population. In our study we were particularly concerned that differences in gear type (Table 1) might bias our results. We opted to include gear type directly into the analysis as a "nuisance" variable, instead

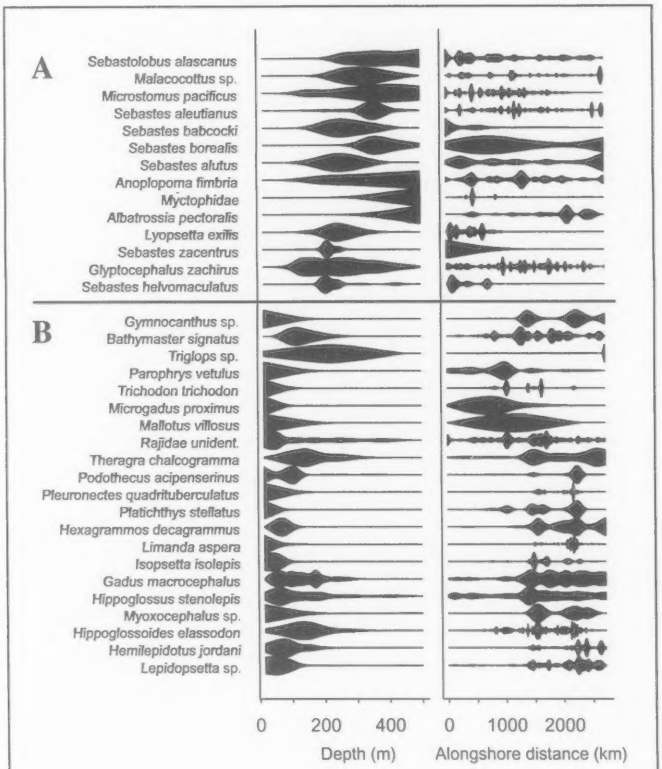

Figure 8

Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (**A**) or negative (**B**) association with the first index of species composition derived from an NMDS ordination of abundances averaged by strata. Widths of dark bands are proportional to average CPUE of a given species. Average CPUE as a function of depth and alongshore distance was estimated by using a scatterplot smoother (cubic smoothing spline). Degree of smoothing was determined by cross-validation for each species separately.

of standardizing the CPUE of each species to a common gear standard prior to analysis because of large uncertainties in the estimation of fishing power coefficients (Munro and Hoff, 1995). The estimated differences among gear types agreed qualitatively with results in Munro and Hoff (1995) for those species for which these authors estimated fishing power. Nevertheless, differences among gear types may have biased some of our results. In spite of these problems, the survey data used in our study provided the best available indicator of relative changes in species composition and distribution for many species of ecological or commercial interest.

The observed trends in species richness, diversity, and biomass, as well as in the CPUE of individual species, showed that depth is an important gradient structuring the groundfish community in the GOA, and that the shelf break and upper slope (at 150–300 m) is a particularly important depth range. Strong depth-dependent gradients are found in many other demersal fish communities inhabiting shelf and upper slope regions (Colvocoresses and Musick, 1984; Gomes et al., 1992; Blaber et al., 1994; Fujita et al., 1995; Jay, 1996; Farina et al., 1997; Mahon et al., 1998). Distinct depth preferences of many individual species (Fig. 8) result in a turnover of species along the depth gradient and lead to the observed patterns in richness, diversity, and biomass. Similar to the altitude gradient in terrestrial environments (Brown and Lomolino, 1998), depth appears to be the major ecological gradient structuring benthic communities in the ocean from shallow, nearshore areas (Mueter and Norcross, 1999) to the abyssal plain (Merrett, 1992).

Our results suggest a pronounced peak in species richness, diversity, and total biomass at intermediate depths. Species richness as well as biomass of demersal fish com-

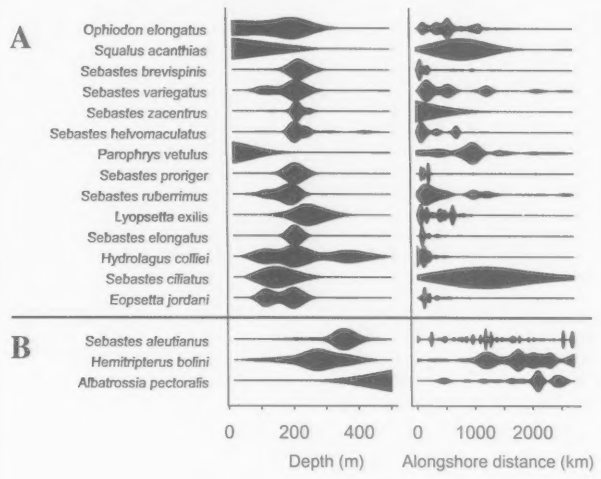

Figure 9

Distribution of CPUE by depth and alongshore distance for all species that had a strong positive (**A**) or negative (**B**) association with the second index of species composition derived from an NMDS ordination of abundances averaged by strata. For details see Figure 8.

munities are generally higher on the continental shelf than on adjacent slope regions, reflecting a strong gradient with depth (Day and Pearcy, 1968; Colvocoresses and Musick, 1984; Farina et al., 1997). In contrast to our results for the GOA, these studies did not find peaks in richness or biomass at intermediate depths. This may have been partly the result of aggregating data into relatively large depth ranges in those studies (and the associated loss in resolution), whereas our study examined patterns in richness and biomass along a continuous depth gradient.

We suggest that the high biomass of demersal fishes near the shelf break (in particular the biomass of flatfishes, rockfishes, and gadids) reflects favorable feeding conditions at this depth range. Favorable feeding conditions may result from enhanced benthic productivity or availability of suitable prey at this depth. The region along the shelf break and over the upper slope has high primary productivity that may be driven by shelf-break fronts, seasonal upwelling, strong alongshore currents, and tidal mixing (Parsons, 1986). Shelf-break fronts have frequently been observed in the GOA (Weingartner[2]) and can enhance phytoplankton and zooplankton biomass, particularly when coupled with upwelling (Mann and Lazier, 1991), which is common during the summer in the western GOA (Reed and Schumacher, 1986). We speculate that increased production in the water column becomes available to the benthos when sinking particles are consumed by larger organisms such as shrimp or euphausiids, which are often concentrated near the shelf break and are consumed by demersal fish (Mackas et al., 1997; Robinson and Gomez-Gutierrez, 1998). The most abundant demersal fishes in the GOA, arrowtooth flounder and walleye pollock, as well as several rockfish species, have been shown to feed near or off the bottom on euphausiids, mysids, copepods, shrimps, and other fishes (Yang, 1993). Thus, a region of enhanced benthic productivity near the shelf break is consistent with the total biomass of groundfish being highest just inshore of the shelf break between 150 and 200 m (Fig. 6).

In addition to depth (or elevation), latitude is a major ecological gradient in both marine and terrestrial environments. Demersal fishes on the continental shelf off both the east coast of North America (Mahon et al., 1998) and the U.S. west coast (Jay, 1996) form loose assemblages that are clearly separated by latitude. Although the latitudinal extent of our study region is relatively small, we found strong alongshore (roughly corresponding to longitudinal) differences in community structure from the eastern GOA to the Aleutian Islands, with the steepest gradient between the Yakutat and Kodiak areas. This gradient was apparent in species richness and diversity (Figs. 2 and 4), total CPUE (Fig. 6), and indices of species composition (Fig. 7). The alongshore gradient is perpendicular to the depth gradient, with depth generally increasing in the offshore direction. However, these two variables were moderately correlated (–0.32, ranging from –0.20 to –0.44 in individual years), primarily due to the larger number of shallow stations in the western part of the study area and a relative lack of shallow stations in Southeast Alaska.

[2] Weingartner, T. J. 2000. Personal commun. Institute of Marine Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775.

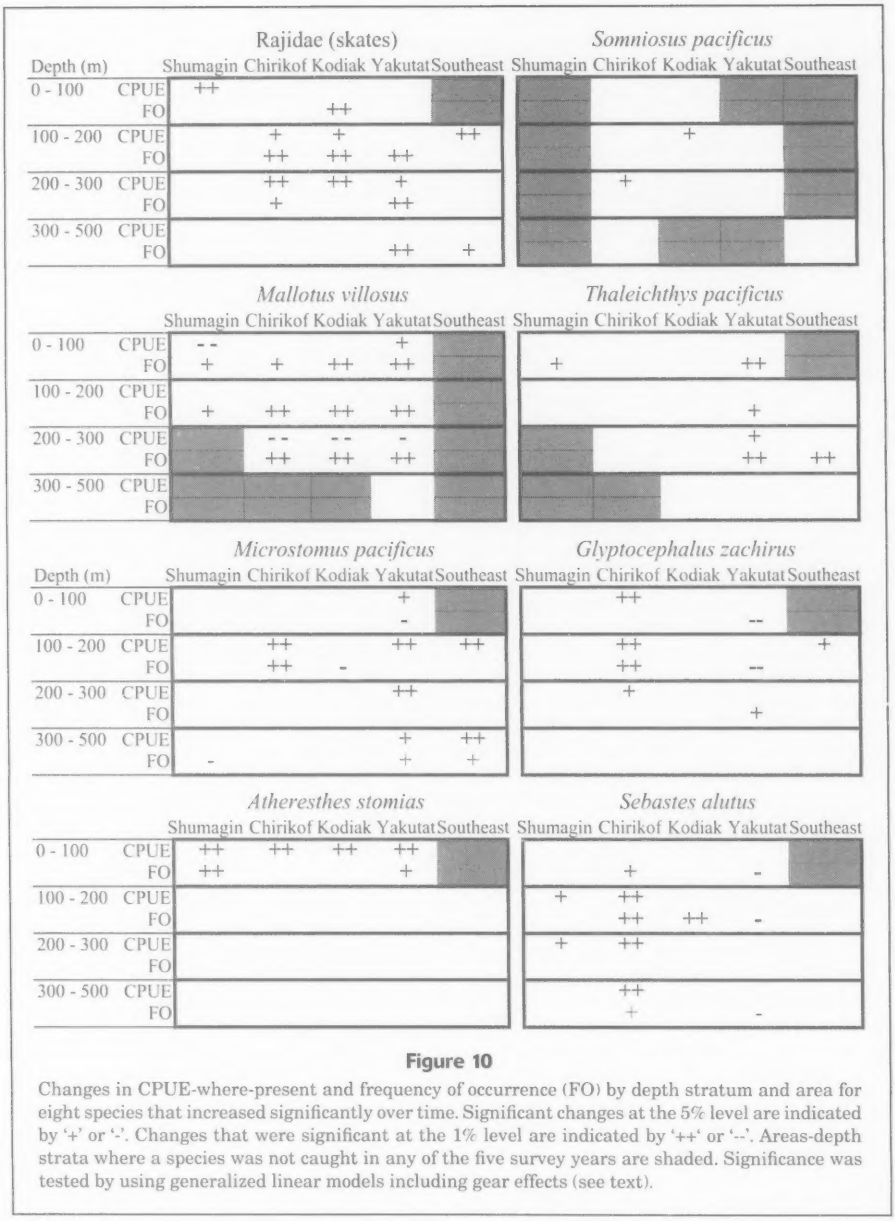

Figure 10

Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for eight species that increased significantly over time. Significant changes at the 5% level are indicated by '+' or '-'. Changes that were significant at the 1% level are indicated by '++' or '--'. Areas-depth strata where a species was not caught in any of the five survey years are shaded. Significance was tested by using generalized linear models including gear effects (see text).

Therefore, the alongshore trends may be partly due to differences in the distribution of sampling depth between the eastern and western GOA resulting from differences in topography. Nevertheless, we do not believe that the magnitude of correlations (Table 3) presents a serious problem for the general patterns that were observed for CPUE, diversity, and species composition.

Alongshore patterns in CPUE (Figs. 5 and 6) indicate a higher biomass of demersal fishes in the western GOA, particularly in the Kodiak Island area. If the higher biomass is related to the availability of food, this pattern may reflect higher benthic productivity in the Kodiak Island region. There are several pieces of evidence that suggest a higher productivity in this region. First, there is a higher benthic biomass and productivity of infaunal organisms on the Chirikof and Kodiak shelf, compared with the Yakutat and Southeast areas (Semenov, 1965, as cited in Feder and Jewett, 1986). Second, enhanced primary productivity in the western GOA is evident in estimates from coastsl zone color scanner (CZCS) data and from more

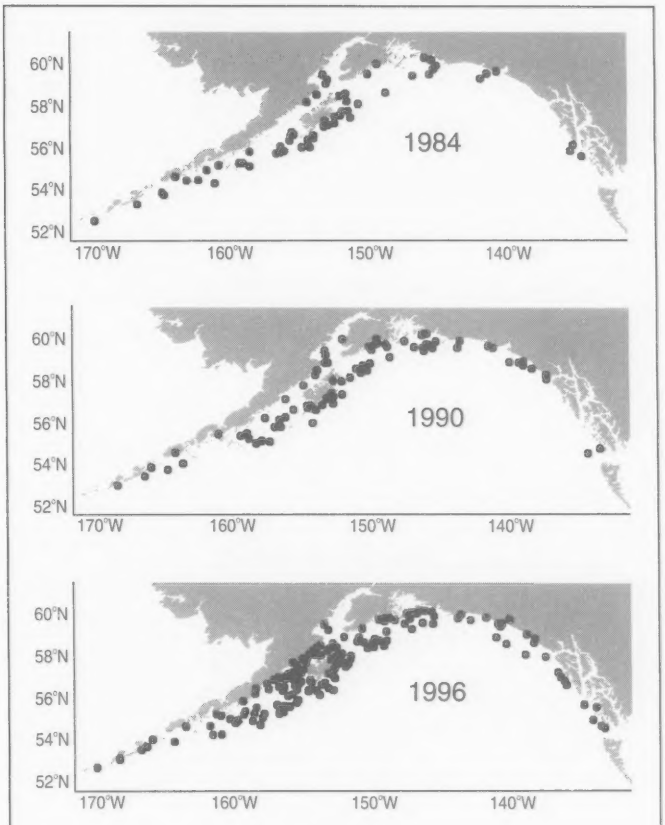

Figure 11

All sampling locations (•) where CPUE of skates (Rajidae) exceeded 300 kg/km^2 in 1984, 1990, and 1996.

recent SeaWifs data (Falkowski et al., 1998, see web site: http://seawifs.gsfc.nasa.gov/SEAWIFS.html). Third, the east–west gradient in productivity and biomass is consistent with differences in upwelling, which is generally more pronounced and more frequent in the western GOA (Reed and Schumacher, 1986). Fourth, the presence of strong tidal currents in the vicinity of Kodiak Island (Kowalik[3]) (see also Isaji and Spaulding, 1987) may further enhance demersal productivity (Mann and Lazier, 1991). Fifth, strong alongshore currents, advection, and nutrient input from major rivers may contribute to a higher productivity in the western GOA and around Kodiak Island. Finally, lower productivity in the eastern GOA may be related to the limited shelf area in this part of the Gulf. Broader shelf areas such as that in the central Gulf of Alaska around Kodiak Island are generally believed to be more productive because of increased nutrient enrichment.

There is evidence from many areas around the world that high productivity is associated with a high biomass of demersal fishes and vice versa. For example, Farina et al. (1997) showed that on the continental shelf and upper slope in the Mediterranean Sea upwelling areas with high primary productivity correlate with a high biomass in the upper trophic levels, including demersal species, and with low species diversity. In contrast, low productivity areas have the greatest species richness and a smaller biomass of demersal fish. Our study suggests that the same general patterns observed by Farina et al. (1997) may hold for the continental shelf and upper slope of the GOA. The productive western GOA is characterized by a high demersal biomass and relatively low species diversity, which is attributable to the presence of a few highly abundant species of flatfish and gadids (including arrowtooth flounder, Pacific cod, walleye pollock). In contrast, the eastern GOA appears to be less productive and is characterized by a low biomass of demersal fishes and high species diversity, due to the presence of a large number of rockfish species with relatively low abundances.

[3] Kowalik, Z. 2000. Personal commun. Institute of Marine Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775.

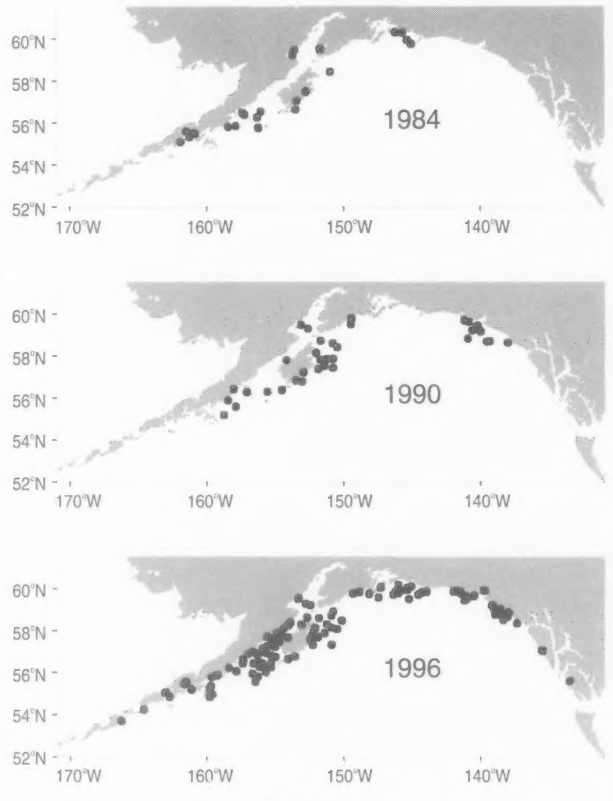

Figure 12

All sampling locations (•) where capelin (*Mallotus villosus*) were caught in 1984, 1990, and 1996.

In contrast to strong spatial and depth gradients, there was little evidence for strong temporal gradients in the GOA groundfish community between 1984 and 1996, except for the pronounced increase in total CPUE and a potential decrease in species diversity after 1993. The species composition of the groundfish community in the GOA, as reflected in our indices, has remained relatively stable from 1984 through 1996. Furthermore, a visual comparison of the indices mapped by year (not shown) suggests that relative species composition is characterized by spatial patterns that were stable from 1984 to 1996. Similarly, no apparent shifts in individual species distributions were found. The apparent stability of spatial patterns in the GOA may simply reflect stability in species composition over the time period of the study, as well as a period of relatively moderate variations in the physical environment. It also suggests that recent levels of fishing may not have had a strong impact on the relative species composition, or possibly had a stabilizing effect. The observed composition of the groundfish community, which is currently dominated by relatively long-lived species, may also contribute to its own stability.

Some of the most pronounced changes over time occurred in noncommercial species such as skates and capelin (Fig. 10). Whether these changes are directly or indirectly linked to fishing or are the result of environmental changes is currently unknown. Interestingly, capelin decreased in abundance in some areas and depth ranges but have been caught at an increasing proportion of the sampling stations in more recent surveys. These changes appear to reflect a "spreading out" of the population at relatively fixed numbers, possibly in response to the increasing abundance of large predatory fishes.

Other studies of groundfish communities have documented relatively stable spatial patterns in species composition over time periods of 10–20 years (Colvocoresses and Musick, 1984; Gabriel, 1992; Gomes et al., 1992; Jay, 1996). In contrast, Gomes et al. (1995) observed a sharp decline in the biomass and abundance of a number of commercial groundfish species on the Newfoundland-Labra-

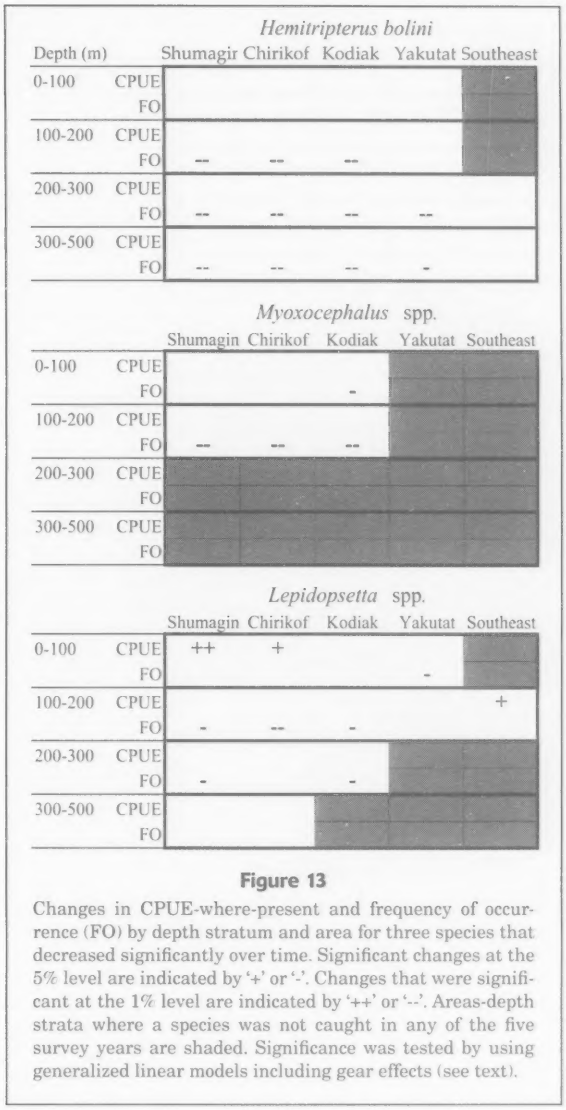

Figure 13

Changes in CPUE-where-present and frequency of occurrence (FO) by depth stratum and area for three species that decreased significantly over time. Significant changes at the 5% level are indicated by '+' or '-'. Changes that were significant at the 1% level are indicated by '++' or '--'. Areas-depth strata where a species was not caught in any of the five survey years are shaded. Significance was tested by using generalized linear models including gear effects (see text).

dor shelf from 1978 to 1991 and dramatic changes in the spatial distribution of groundfish assemblages after 1987. They attributed the changes primarily to intense exploitation, although environmental effects were likely at work as well. Similarly, on the continental shelf off Northwest Spain, significant decreases in commercial groundfish species, and a concurrent increase of several noncommercial species, can be attributed to a combination of fishing and environmental changes (Farina et al., 1997).

The recent period of stability in the GOA can be contrasted with a period of dramatic changes in the late 1970s and early 1980s that affected many parts of the North Pacific ecosystem including groundfish communities (e.g. Beamish, 1995). There is strong evidence of a shift in species composition of at least the nearshore demersal communities during this time period (Piatt and Anderson, 1996; Anderson and Piatt, 1999; Mueter and Norcross, 2000). Whether similarly dramatic changes occurred in offshore demersal communities is not known due to the lack of long time series for most species.

Estimated biomass trends for important commercial species based on recent stock assessment data (NPFMC[1]) and historical surveys (Ronholt et al.[4]) suggest that the

[4] Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1978. Demersal fish and shellfish resources of the Gulf of Alaska from Cape Spencer to Unimak Pass 1948–1976: a historical review. Proc. rep., vols. 1–3, 872 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA.

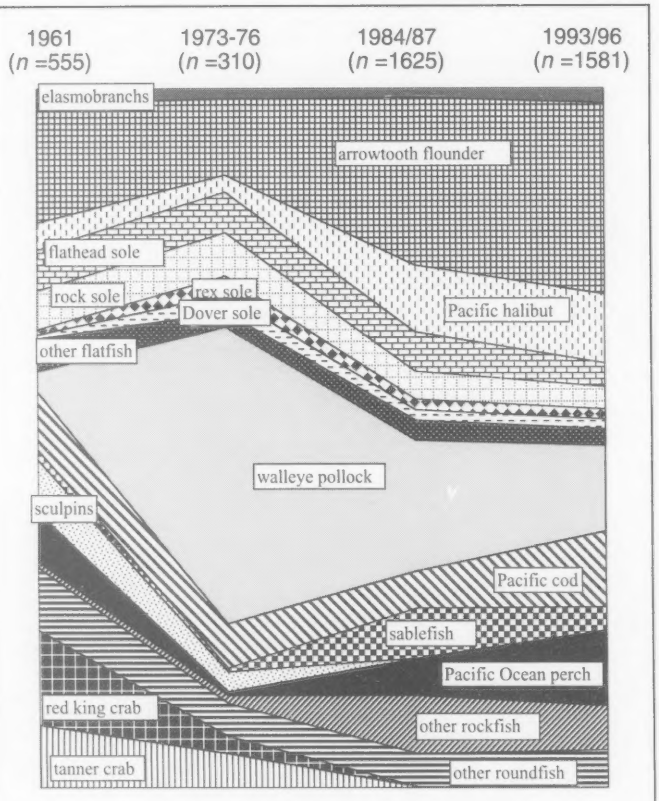

Figure 14

Proportional biomass composition of Gulf of Alaska groundfish communities from the 1960s through the 1990s as estimated from bottom trawl surveys. All surveys used similar gear, but sampling in 1961 and 1973–76 was limited to 0–400 m depth. Total number of hauls is indicated below each time period.

composition of the groundfish community on the shelf and upper slope has changed substantially since the early 1960s. Resource assessment surveys were conducted in 1961 and 1973–76 with similar gear and covering much of the same area that was sampled during the later surveys. Survey data from the 1960s and 1970s have to be interpreted carefully because the sampling design, gear, and the spatial coverage of these surveys differ from the surveys done in the 1980s and 1990s.[4] In particular, no stations below 400 m or east of 136°W were sampled in the early surveys. In spite of these caveats, changes in species composition among surveys are likely to reflect actual changes, at least for taxa that occur primarily above 400 m and west of 136°W. The data suggest a dramatic decrease in the relative abundance of red king crab (*Paralithodes camtschaticus*) and Tanner crab (*Chionoecetes* spp.), which together accounted for 22% of total CPUE in 1961, and for less than 1% after the 1970s (Fig. 14). The data indicated that walleye pollock became the dominant species in the mid-1970s, peaked in the early 1980s, and has declined in relative abundance since then. Arrowtooth flounder replaced walleye pollock as the dominant groundfish species in the 1980s and 1990s. Pacific Ocean perch and other rockfishes have increased substantially in biomass since the 1970s. Sablefish and Pacific halibut, two of the commercially most valuable species, made up a substantially larger proportion of the total CPUE in the 1980s and 90s compared to earlier decades (Fig. 14). The relative abundance of sculpins declined from about 8% in the early 1960s to less than 0.1% in the 1980s and 1990s. The observed difference is likely to reflect a real decline in sculpin abundance of several orders of magnitude between the 1960s and 1980s. The decline appears to continue into the 1990s, as suggested by a decrease in the frequency of occurrence and biomass of two of the most abundant sculpin taxa (bigmouth sculpin and *Myoxocephalus* spp., see Fig. 13, Table 2).

The observed increase in overall groundfish biomass in the GOA from the 1980s to the 1990s (Fig. 6) is consistent with increases in the productivity of the northeast Pacific

Ocean between the period of the 1960s and 70s and the 1980s and 90s. Polovina et al. (1995) suggested that the increase in primary and secondary productivity in the NE Pacific Ocean resulted from a shoaling of the mixed layer in the GOA by 20–30% associated with variations in the strength and position of the Aleutian low pressure system from the late 1970s to the late 1980s. Over the same time period large increases occurred in chlorophyll *a* levels (Venrick, 1995), zooplankton stocks (Brodeur and Pearcy, 1992; Brodeur et al., 1996), and upper trophic level species (Brodeur and Ware, 1995; Francis et al., 1998). Our study suggests that there has been a parallel increase in the biomass of demersal fish communities on the GOA shelf and upper slope since 1984, in response to the overall increase in productivity in the NE Pacific Ocean.

Given the increasing emphasis on ecosystem-based management, managers will have to rely on a variety of indicators in addition to traditional single-species biomass estimates to assess the status and health of an ecosystem (Yaffee et al., 1996). Indices of species composition like those used in this study, as well as survey-based assessments of noncommercial species, provide indicators that can help researchers in assessing changes in the community and can help managers in responding to such changes in a timely fashion.

Species richness and diversity are particularly simple, yet potentially very useful indices. The concept of marine biodiversity has received considerable attention in recent years (NRC, 1995) and should be included in planning and policy-making (Bengtsson et al., 1997). There is some evidence that bottom fishing can reduce the diversity of benthic communities (Collie et al., 1997) and, in turn, that changes in diversity can impact ecosystem function and productivity (Naeem et al., 1994). There was some indication in our study that the number of species and the diversity of the groundfish community in the GOA as measured by the Shannon-Wiener index decreased between 1993 and 1996 (Fig. 4). Although gear effects may have confounded differences among earlier surveys, the same gear and identical survey designs were used in both 1993 and 1996; thus the differences in species richness and diversity cannot be attributed to sampling effects and merit further study. The simple diversity indices used in our study were primarily chosen for practical considerations. Other indices, e.g. indices of beta-diversity, may be more appropriate for describing diversity of marine ecosystems and should be explored.

Multivariate techniques that summarize the major variation in species composition with a small number of indices (dimensions) provide another useful tool for monitoring changes in groundfish communities. Such indices provide sensitive indicators of change in community structure and can identify general trends that may not be apparent when using univariate measures (Austen and Warwick, 1989). The indices reduce the noise from random fluctuations of many individual stocks and the resulting "signal" may be used to test statistically for differences in species composition among areas or time periods, as well as helping to identify those species that show significant trends.

Another important part of an ecosystem approach to management is the monitoring of the abundance of noncommercial species, in addition to commercial species. Changes in the abundance of skates, sculpins, and other noncommercial species are examples of potentially important trends that may go undetected if management agencies focus on the assessment of commercial species only. Although these species comprise a small proportion of total biomass, such trends may be an early indication of changes in the groundfish community due to changes in the environment or fishing. Such monitoring, along with the monitoring of environmental variables, will further help to understand how and why groundfish communities change in response to environmental variation.

Current fisheries management often fails to account for the ecological complexities inherent in fish communities (Roberts, 1997). This is hardly surprising because of the focus of most stock assessment on individual stocks and on stock-recruitment relationships. Prediction becomes increasingly difficult as other species and environmental relationships are added to models. Nevertheless, the complexities should not discourage researchers from trying to understand species relationships and the response of species and communities to environmental variation and harvesting.

Knowledge of such relationships can improve management in several ways. First, it can help to explain why stocks are fluctuating in particular ways and help managers devise management strategies that take into account such fluctuations. Second, it can improve our understanding of multispecies or community-level relationships and can lead to better assessment methods that take such relationships into account. Third, it can lead to predictive hypotheses that can be explored and tested through rigorous research programs and adaptive management procedures. Ultimately, improved understanding of ecosystem processes will improve fisheries management only if it can reduce uncertainties in prediction. Thus the challenge remains to develop improved models that account for species relationships and environmental influences.

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Abstract–Life-history dynamics of pinfish (*Lagodon rhomboides*) were examined from data derived from random-station surveys conducted in Tampa Bay and adjacent Gulf of Mexico waters during 1993–97. In addition, patterns in spatial distribution and abundance in Gulf of Mexico waters were investigated. Ages determined from whole otoliths ranged from 0 to 7 years, and von Bertalanffy growth models for males and females were not significantly different. Von Bertalanffy growth model parameters were L_∞=219.9 mm SL, k =0.33/yr, and t_0 =–1.10 years for all fish combined. High gonadosomatic indices during October–December indicated that some spawning may occur in Tampa Bay. Estimated lengths at 50% maturity were 132 mm SL for males and 131 mm SL for females. Total instantaneous mortality rates derived from the Chapman-Robson estimator ranged from 0.88 to 1.08/yr, and natural mortality was estimated to be 0.78/yr. In Gulf of Mexico waters, pinfish catch rates declined with increasing depth, and most pinfish were caught in <17 m of water. Length distributions showed that pinfish segregate by size with increasing depth.

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Age, growth, mortality, and distribution of pinfish (*Lagodon rhomboides*) in Tampa Bay and adjacent Gulf of Mexico waters

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The pinfish (*Lagodon rhomboides*) is an ecologically important sparid that inhabits estuarine and offshore waters of the United States from Massachusetts to Texas (Darcy, 1985). Young-of-the-year pinfish are predators on a range of invertebrates in estuaries, often to the degree that entire assemblages of macrobenthic fauna are affected (Young et al., 1976; Young and Young, 1977; Nelson, 1978). They also consume seagrasses during their estuarine phase, which makes them an important link between primary and secondary production (Stoner, 1982; Weinstein et al., 1982; Montgomery and Targett, 1992). Both young-of-the-year and adult pinfish are prey for other fishes (Gunter, 1945; Darnell, 1958; Carr and Adams, 1973; Seaman and Collins, 1983) and are used as bait for many recreationally and commercially important species.

Despite their ecological and economical importance, the population biology and dynamics of pinfish in Florida have not been adequately examined. Most knowledge about growth (Reid, 1954; Caldwell, 1957; Hellier, 1962; Nelson, 1998), distribution and migration (Caldwell, 1957; Hansen, 1970; Nelson, 1998), and mortality (Nelson, 1998) comes from studies of young-of-the year pinfish in estuaries. The only information available on older individuals comes from estuarine studies that describe size and age at spawning (Caldwell, 1957; Hansen, 1970), gross fecundity (Caldwell, 1957), and longevity and size at age (Hansen, 1970). However, that information may contain biases because sampling did not extend into offshore waters where larger, and presumably older, pinfish are thought to occur, particularly during cooler months (Darcy, 1985).

In this study, age, growth, mortality, and maturation of pinfish were evaluated by studying data from multigear fisheries-independent surveys conducted in Tampa Bay, Florida, and in offshore waters off west-central Florida. In addition, patterns in abundance and spatial distribution of pinfish in the Gulf of Mexico were examined.

Methods

Biology

Pinfish for aging, maturity, and mortality analyses (n=711) were collected opportunistically from fall 1993 to spring 1997 during multiple fisheries surveys conducted in Tampa Bay and offshore Gulf waters by the Florida Marine Research Institute (Fig. 1). Pinfish from Tampa Bay were collected primarily during multigear seasonal (spring and fall) and monthly fisheries-independent surveys designed to estimate relative abundance of small estuarine fishes and evaluate life-histories parameters of large estuarine fishes (Table 1). During the surveys, sites were chosen by randomly selecting 1″ latitude × 1″ longitude microgrids, representing the site to be sampled, within randomly selected 1′ latitude ×

Table 1

Length summary statistics (by area, year, and gear) for pinfish collected during biological sampling. Exp. gill net = experimental gill net.

Year	Gear	Stretched mesh (mm)	Pinfish SL (mm)			
			Minimum	Maximum	Mean	*n*
Tampa Bay						
1993	trammel net	76, 305	179	255	211.8	31
1995	exp. gill net	50–152	170	185	180.0	3
	183-m seine	38	73	202	121.1	50
	trammel net	76, 305	173	216	191.4	8
	21-m seine	3.2	73	150	112.1	24
	61-m seine	25.4	72	165	132.6	19
1996	183-m seine	38	66	207	126.9	313
	purse seine	50	100	181	125.9	34
	trammel net	76, 305	203	203	203.0	1
	21-m seine	3.2	34	174	89.0	28
	hook and line	—	198	205	202.0	3
1997	183-m seine	38	83	155	111.3	62
	purse seine	50	91	156	108.9	16
	21-m seine	3.2	25	104	71.7	18
Gulf of Mexico						
1996	hook and line	—	116	149	135.2	17
1997	bottom trawl	254	95	175	128.8	84

1′ longitude grids. At each site, gears were deployed with standardized procedures (see Nelson [1998] and Tremain and Adams [1995] for detailed description of the survey design and deployment techniques). Selected individuals were immediately placed on ice for transport and frozen whole at the laboratory.

Pinfish from the Gulf of Mexico were collected primarily during a bottom-trawl survey conducted in spring in the Gulf of Mexico to document baitfish abundance and distribution. The Gulf trawl survey was conducted during April from 1994 to 1997 at stations randomly selected along line transects randomly placed perpendicular to the west coast of the Florida peninsula adjacent to Tampa Bay. At each station, a 19.8-m, 254-mm stretched-mesh modified ballon trawl with 25.4-mm codend liner and 2.2-m^2 China V-doors was towed at approximately 3 knots for 30 min during daylight hours in depths ranging between 6 and 31 m. At each station, trawl catches were sorted by species, counted, weighed collectively, and 50 individuals per haul were measured to the nearest 1 mm fork length (see Pierce and Mahmoudi [2001]) for a detailed description of the survey design). Depth (m) at the start and end of the trawl tow and surface salinity and temperature were recorded at all stations. To match data collected from the Tampa Bay samples, all length data were converted to standard length by using conversion equations derived from this study. Individual fish were immediately frozen whole and returned to the laboratory. Occasionally, supplemental samples were collected by hook-and-line fishing in Tampa Bay and the offshore waters (Table 1).

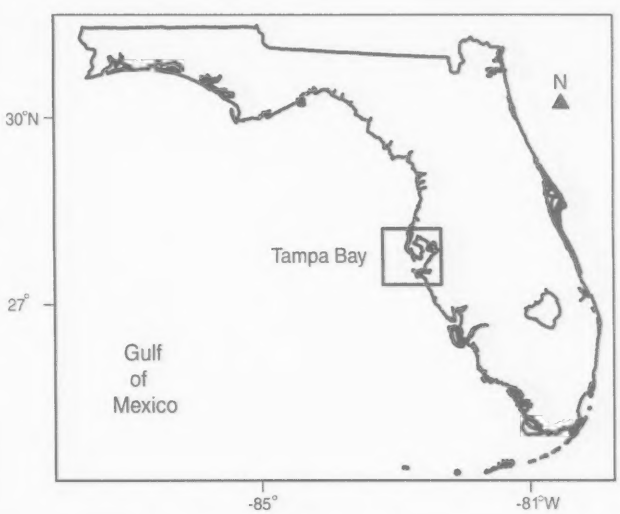

Figure 1

Maps of Florida showing study area.

In the laboratory, standard length (SL ±1 mm), fork length (FL ±1 mm), total length (TL ±1 mm) and total

weight (TW ±0.01 g; measured after each individual was blotted dry) were recorded for all thawed, undamaged individuals. Gonads were excised from a subsample of individuals (~80%) of each collection, identified macroscopically (and microscopically if needed) as ovaries or testes, blotted dry on a paper towel, and weighed (±0.01 g). Seasonal conversion equations for length measurements were generated by least-squares regression (SAS, 1990a).

Age and growth

Sagittal otoliths for aging studies were excised, cleaned of extraneous tissue, and stored dry in vials. Otolith length was measured under a binocular dissecting microscope at 10× with a calibrated ocular micrometer, and an otolith length (mm) versus fish standard-length relationship was derived by using least squares regression. For age determination, one whole otolith (either left or right) was placed on black velvet to enhance the visibility of opaque zones, submerged in a 60% glycerin solution, and viewed at 32× with reflected light. Otolith edges were classified as either opaque or hyaline to determine time of opaque ring formation. The number of opaque rings was considered to equal the age in years of the pinfish. Age determinations were repeated three times on all whole otoliths. If two of the three age readings were in agreement, the value was accepted. If age varied between all readings, the structure was not included in the analysis. The accuracy with which whole otoliths can be used to age pinfish was confirmed by comparing whole otolith ages from a subsample of the largest pinfish to age readings made on thin sections of the same otoliths. Methods of Hood and Johnson (1999) were used to section otoliths. To verify the consistency of the opaque ring counts, a random subsample (13%) of all whole otoliths was aged once by an experienced second reader and the results were compared to the final age determination. Pinfish larvae are present off the west coast of Florida between November and February (Darcy, 1985); therefore a 1 January birthdate was assumed for all pinfish. Age in years was designated with a decimal extension that represented the date of capture in days from the 1 January birthdate.

Growth was modeled by fitting length-at-age for all years combined to the von Bertalanffy equation:

$$L_{i,t} = L_\infty * \left(1 - \exp^{(-k*(age - t_0))}\right) + \varepsilon_{ij},$$

where $L_{i,t}$ = the standard length of the i th individual at age t;
L_∞ = the asymptotic maximum length;
k = a growth constant;
t_0 = the hypothetical age at which length is zero; and
$\varepsilon_{ij}s$ = independent, identically distributed, normal random errors.

Parameters L, k, and t_0 were estimated by using SAS nonlinear regression (Proc NLIN) with the Marquardt method (SAS Institute, 1990b). Lack of fit was assessed by using residuals plots (Bates and Watts, 1988).

Growth-rate differences between sexes were investigated by using an approximate randomization test to compare growth curves (Helser, 1996). Essentially, differences were investigated by comparing an observed test statistic to an empirical probability density function of a test statistic under the null hypothesis of no difference. The observed test statistic for pinfish was developed by fitting the von Bertalanffy growth functions to length-at-age data for sexes combined and to length-at-age for each sex separately. The sums of the residual sum of squares from the two sex-specific models were then used to calculate the observed test statistic

$$t(x_0) = \sum_{i,t} (l_{i,t} - \hat{l}_t)^2 - \sum_{i,t,p} (l_{i,t,p} - \hat{l}_{t,p})^2,$$

where $t(x_0)$ = the test statistic;
l_t = the predicted length-at-age for all sexes combined; and
$l_{t,p}$ = the predicted length-at-age for each sex (p=1,2) (Helser, 1996).

To generate the empirical probability density function (pdf), length-at-age data for both sexes were pooled and then assigned randomly without replacement to two groups with sample sizes equal to the original number of observations per sex. Growth curves were then fitted separately to the length-at-age data of the randomized groups, and the test statistic under the null hypothesis of no difference was calculated as

$$t(x) = \sum_{i,t} (l_{i,t} - \hat{l}_t)^2 - \sum_{i,t,p} (l^*_{i,t,p} - \hat{l}^*_{t,p})^2,$$

where $t(x)$ = the difference in residual sum of squares between the von Bertalanffy fits to the entire pooled data set and von Bertalanffy fits to the randomized groups (denoted by *).

The randomization procedure was repeated 1000 times to obtain the pdf of $t(x)$. The null hypothesis of no difference was rejected if $t(x_0) > t(x)$ at α=0.05.

Reproduction, sex ratios, and maturity

Gonads excised from selected individuals were classified macroscopically as either immature or mature by using the maturation criteria of Nikolsky (1963) and Cody and Bortone (1992). Seasonality of reproduction was determined by noting when changes in the gonad condition took place. A gonadosomatic index (GSI) was calculated to show changes in gonad weight in relation to gonad-free total body weight. The index was computed as

$$GSI = \textit{gonad weight}/(\textit{total body weight} - \textit{gonad weight}) \times 100.$$

Length at 50% maturity was estimated for pinfish captured during the season of gonadal maturation. The prob-

ability of pinfish being mature was modeled as a logistic function of the following form:

$$P_i = \frac{\exp^{(\alpha+\beta*x_i)}}{1+\exp^{(\alpha+\beta*x_i)}} + \varepsilon_i,$$

where P = the response probability;
x = the standard length (mm) of the i th fish;
α = the intercept;
β = the slope coefficient of standard length; and
ε_i = the error term.

Model regression coefficients were estimated using maximum likelihood (SAS, 1997). Goodness-of-fit was assessed with the chi-square test.

Chi-square analyses were used to test for deviations from a theoretical 50:50 sex ratio.

Length-weight relationships

Because of the seasonality of reproduction, data on body length and weight were separated into two groups representing two time periods to construct length-weight relationships that reflected seasonal changes in gonad weight. Data collected during March–August composed the data group representing the spring–summer period, and data collected during September–February composed the data group representing the fall–winter period. Seasonal regression equations for $\log_{10}$-transformed standard length and body weight (total and gonad-free weight) were generated by the least-squares regression. One-way analysis of covariance (Sokal and Rohlf, 1981), conducted by using SAS PROC MIXED (Littell et al., 1996), was used to test for differences between regression slopes and adjusted means of the length-weight relationships by sex and season.

Mortality

Total instantaneous mortality (Z) was estimated in Tampa Bay and the Gulf of Mexico from pinfish numbers-at-age data by using the Chapman-Robson equation for survival (S) estimation:

$$-Z = \ln(S) = \ln\left(\frac{\sum_{i=1}^{n} x_i}{n+\sum_{i=1}^{n} x_i - 1}\right),$$

where ln = the natural log;
x_I = the number of years the i th fish is older than the age-at full-recruitment;
S = annual survival; and
n = the total number of fully recruited fish (Chapman and Robson, 1960).

The variance of Z was estimated from the variance of S by

$$V(Z) = \frac{S(1-S)^2}{n*S^2}$$

(Jensen, 1985). The Chapman-Robson estimator was used because it is more robust to sample size variation in numbers-at-age (Jensen, 1996; Murphy, 1997).

In addition to Z, natural mortality (M) of pinfish was estimated by using a multiple regression equation relating M to L_∞ (TL in cm) and k (per yr) of the von Bertalanffy equation, and to mean annual water temperature (°C)(Pauly, 1980). To estimate the growth parameters used in the equation, the von Bertalanffy function was refitted to total length and age data. Mean annual water temperature was estimated from temperature data of the Tampa Bay survey.

Distribution

To determine if pinfish catch rates in the Gulf of Mexico were associated with depth, a generalized linear model (McCullagh and Nelder, 1989) was used to model the random trawl catches during the April survey from 1994 to 1997. Catch data were transformed by using $\ln(x+1)$ to stabilize the variance and reduce the influence of sampling variability between tows. Year, average depth of the trawl tow, and their first-order interaction were included in the model. Only depth was analyzed because surface readings of temperature and salinity were thought to not reflect bottom conditions where the trawl tows were made. Size structure of pinfish caught during the Gulf of Mexico survey was also examined by calculating summary statistics (mean and percentiles) of length data to identify patterns related to depth.

Results

Biology

Length-conversion equations are listed in Table 2. All slopes and intercepts were significantly different from zero.

Age and growth

Age determination was based on sagittae from 658 pinfish (66–255 mm SL). Alternating opaque and hyaline zones, which composed an annual growth increment, were evident on whole pinfish otoliths (Fig. 2A). Only 13 otoliths were considered unreadable. Agreement between the number of opaque bands counted on whole otoliths and the number counted on sections of the same otoliths (Fig. 2B) was 96.3% (26/27), indicating that whole otoliths can be used to reliably age pinfish. The high percentage of agreement (89.6%) between the author's final annulus counts and those made by a second reader, and no apparent bias towards a particular aging error, indicated that ages were consistently interpreted.

Plots of the monthly proportions of otolith with opaque edges for pinfish ages 1 to 3 indicated that an opaque ring

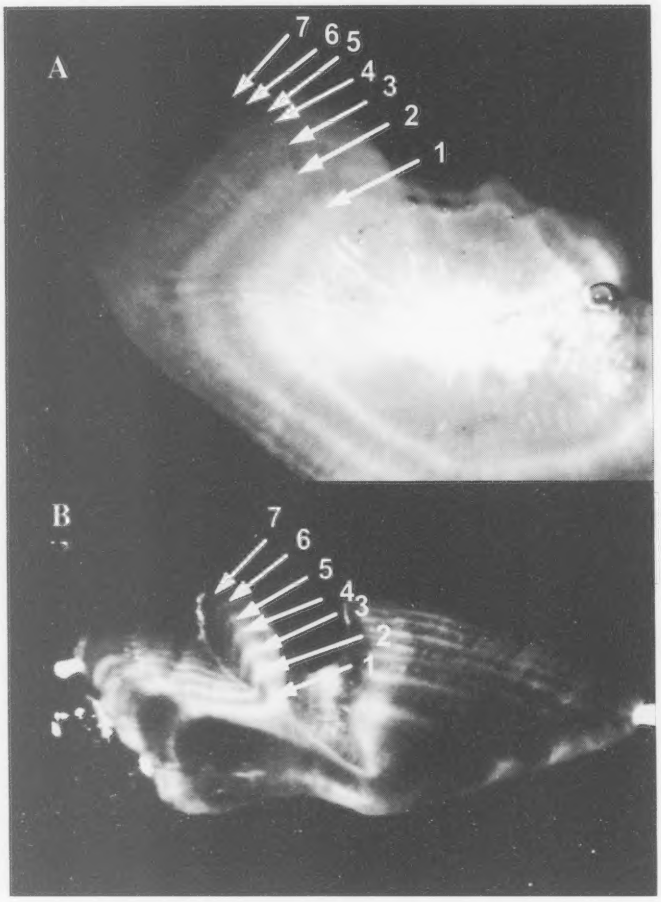

Figure 2

A whole (**A**) and sectioned (**B**) sagitta from a 7-year-old (230-mm-SL) pinfish caught in Tampa Bay in November 1993.

is formed only once a year, during late winter to late spring. Deposition of opaque material began as early as January; it peaked during March, April, or May depending on age; and it was completed, or nearly so, by June (Fig. 3).

A single regression equation characterized the relationship between otolith length (OT in mm) and standard length for a random sample of pinfish 71–230 mm SL (standard errors are in parentheses) used in age analysis:

$$OT = 8.03(1.07) + 0.39(0.008) \times SL; \quad [r^2 = 0.95, n = 132].$$

The intercept and slope coefficients were significantly different from zero ($P<0.001$).

Ages of pinfish ranged from 0 to 7 years (66–255 mm SL) in Tampa Bay and from 1 to 6 years (95–175 mm SL) in the Gulf of Mexico (Fig. 4A). The majority (88.1%) of aged pinfish were ≤2 years. Residual plots from the growth models showed near-random patterns, indicating that the von Bertalanffy model adequately described the growth of male and female pinfish. Results of the randomization test did not indicate a significant difference between male and female growth models ($t(x_0)$=2,691; $p(t(x)>t(x_0))$=0.27); therefore, a von Bertalanffy model was fitted to all pinfish data combined (Fig. 4B, Table 3). Growth rate of pinfish was rapid for the first 1–3 years of life but gradually decreased thereafter (Fig. 4B).

Reproduction, maturity, and sex ratios

Seasonality of reproduction was indicated by monthly changes in the GSIs of all pinfish over time. In Tampa Bay and the Gulf of Mexico, GSIs for males and females were ≤0.5% during the spring and summer months (Fig. 5).

Table 2

Linear regression statistics showing the length conversion and length-weight relationships for pinfish. For the length conversions, the model is $y = \alpha + \beta \times x$. For the weight-length relationships, the model is $\log_{10}(y) = \alpha + \beta \times \log_{10}x$. α is the regression intercept, β is the slope coefficient, r^2 is the coefficient of determination, n is the sample size, MSE is the mean square error, FL is fork length (mm), SL is standard length (mm), TL is total length (mm), GFW is gonad-free body weight, and TW is total body weight (g). SP–SU is spring–summer and FA–WI is fall–winter. All slopes and intercepts were significantly different ($P \leq 0.05$) from zero. Slopes between TW-SL relationships were significantly different ($P \leq 0.01$).

y	x	Season	α	SE(α)	β	SE(β)	r^2	n	MSE
FL	SL	All	2.65	0.368	1.14	0.003	0.996	603	4.736
TL	SL	All	–2.20	0.542	1.33	0.004	0.994	625	13.745
TL	FL	All	–3.73	0.412	1.15	0.003	0.997	591	5.695
GFW	SL	SP–SU	–4.56	0.061	3.04	0.029	0.977	257	0.0020
TW	SL	SP–SU	–4.53	0.045	3.03	0.021	0.983	343	0.0020
GFW	SL	FA–WI	–4.57	0.064	3.07	0.030	0.977	244	0.0024
TW	SL	FA–WI	–4.68	0.043	3.11	0.021	0.987	302	0.0023

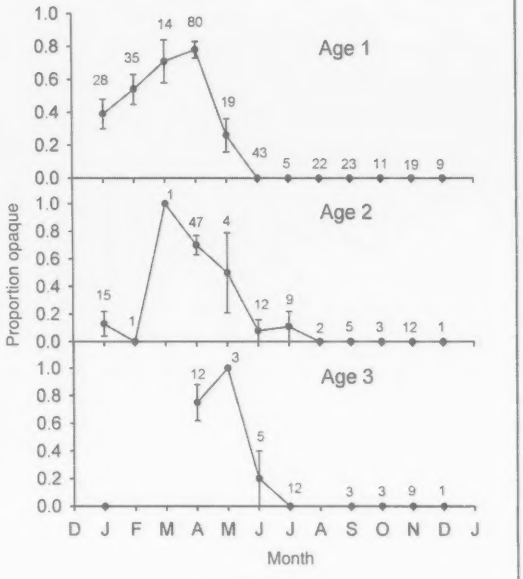

Figure 3

Monthly proportions of whole otoliths with opaque edges for pinfish ages 1–3. ±1 standard error bars are shown.

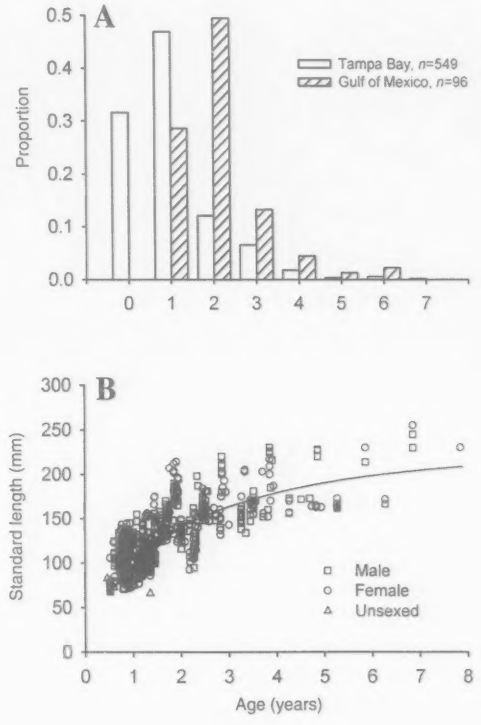

Figure 4

Plots of (**A**) age composition from Tampa Bay and Gulf of Mexico samples and (**B**) von Bertalanffy growth model fitted to standard length and age data for all sexes combined.

GSIs began to increase in October (females) and November (males) in Tampa Bay. The highest GSIs for males and females in Tampa Bay were 5% and 8%, respectively, observed in December. High and moderate GSIs for females and males during January in the Gulf of Mexico indicated continued spawning, but low values in April suggested that spawning ended prior to that month (Fig. 5).

Maturity of male and female pinfish was related significantly to length (male: Wald χ^2=18.8, $P \leq 0.001$; female: Wald χ^2=32.1, $P \leq 0.001$) by logistic equations, and there was no evidence of lack of model fit (male: χ^2=81.1, df=94, P=0.82, max-rescaled r^2=0.38; female: χ^2=109.2, df=121,

Table 3

Estimates of the von Bertalanffy growth parameters for pinfish by sex and for all sexed and unsexed fish combined. MSE is the mean square error, r^2 is the coefficient of determination, and n is the sample size. Asymptotic standard errors are shown in parentheses.

Sex	L_∞	k	t_0	MSE	r^2	n
Male	228.5 (19.733)	0.31 (0.079)	−1.21 (0.331)	517.926	0.57	285
Female	212.0 (16.504)	0.33 (0.082)	−1.16 (0.309)	551.020	0.51	330
All fish	219.9 (12.204)	0.33 (0.055)	−1.10 (0.203)	537.490	0.55	645

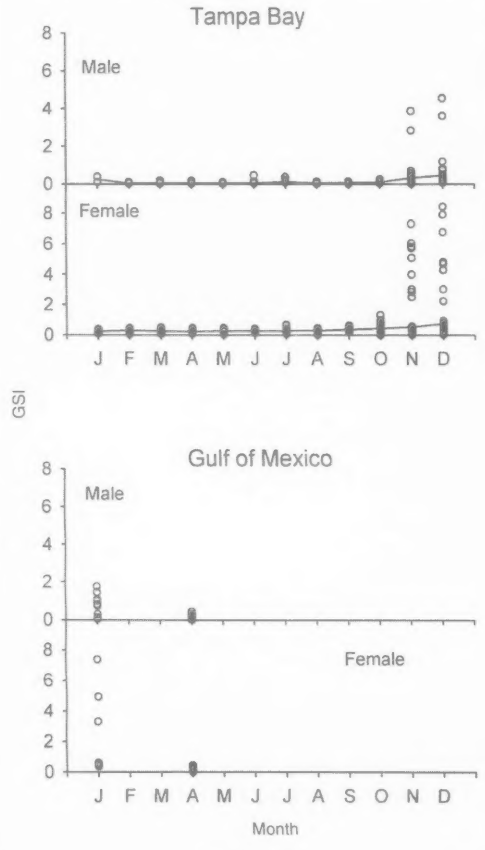

Figure 5

Plots of monthly gonadosomatic indices (GSI) for male and female pinfish from Tampa Bay and the Gulf of Mexico. The solid line connects median values.

P=0.77, max-rescaled r^2=0.60). Parameter estimates (standard error) were α = −7.78 (1.745) and β = 0.06 (0.014) for males, and α = −9.83 (1.721) and β = 0.08 (0.013) for females. The estimates of length at 50% maturity ±95% C.I. were similar for both sexes: 132 ±8 mm SL for males and 131 ±8 mm SL for females. The smallest mature male was 112 mm SL and the smallest mature female was 92 mm SL. The largest immature male pinfish was 245 mm SL and female pinfish was 173 mm SL.

Chi-square tests indicated that sex ratios did not deviate significantly (P>0.05) from unity in any season.

Length-weight relationships

No significant differences (P≥0.10) in slopes or intercepts of standard-length on body-weight relationships were observed between sexes in any period; therefore all data were pooled for the subsequent analyses. Seasonal length-weight regressions for both sexes combined are listed in Table 2 for total and gonad-free body weight. Regression slopes were significantly different between periods only for the standard-length on total-body-weight relationship (P≤0.01). The regression slope was highest in fall–winter, which indicates that pinfish gain more weight per unit increase in length during this period than in spring–summer. Adjusted means for the standard-length on gonad-free body-weight relationship were not significantly different between periods (P>0.05).

Mortality

Based on frequency plots by age, age-at-full-recruitment was age 1 for pinfish in Tampa Bay and age 2 for those in the Gulf of Mexico. Estimates of Z were 1.08/yr for Tampa Bay pinfish and 0.88/yr for the Gulf of Mexico pinfish (Table 4). Estimates of Z for all areas combined, assuming full recruitment at age 2, were intermediate to the Z estimates made for each area separately (Table 4).

The estimate of M was 0.78/yr from Pauly's (1980) multiple regression equation by using L_∞ = 30.1 cm, k=0.31/yr, and mean annual temperature of 24°C.

Distribution

In the Gulf of Mexico, pinfish were captured at 90% (55/61) of sites where trawls were pulled in depths of 6 to 30 m during the baitfish survey (Fig. 6). Catch rates of pinfish in the Gulf of Mexico varied significantly between years and were associated with depth, but the significant interaction term indicated that the relationship between depth and catches varied between years (Table 5). Plots of cumulative proportions of total catches by year showed that most trawl catches (95%) occurred in waters <15 m during the 1994, 1995, and 1997 surveys, but in 1996, 95% occurred in waters <17 m (Fig. 7A).

Length summary plots for pinfish caught during the baitfish survey showed that pinfish became segregated by size as depth increased. Median length increased from 109 mm SL in the 6–10-m depth range to 152 mm SL in the 26–30 m depth range (Fig. 7B). The smallest (80-mm-SL)

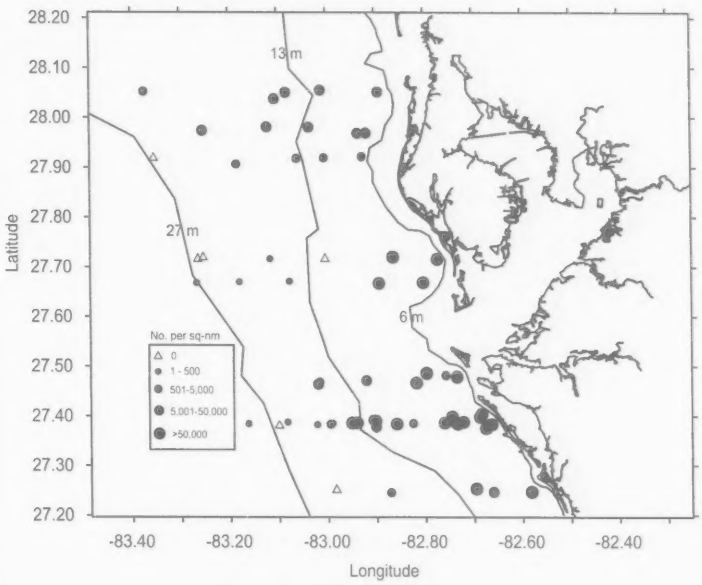

Figure 6

Map of distribution of pinfish catches from the baitfish trawl survey in Gulf of Mexico waters adjacent to Tampa Bay, 1994–97. Latitude and longitude values are given in decimal degrees.

Table 4

Estimates of annual survival (S) and total instantaneous mortality (Z) of pinfish determined by using the Chapman-Robson (1960) estimator for Tampa Bay, the Gulf of Mexico, and both areas combined. n_r is the sample size at each age of full recruitment and n_a is the number of age classes included.

	Age (yr) at full recruitment	n_r	n_a	Estimate		Variance	
				S	Z	S	Z
Tampa Bay (n=549)	1	379	7	0.34	1.08	0.0004	0.0033
Gulf of Mexico (n=96)	2	70	5	0.41	0.88	0.0020	0.0120
Combined (n=645)	2	189	6	0.40	0.90	0.0008	0.0043

and the largest (203-mm-SL) pinfishes were captured in the 6–10 m and 11–15 m depth ranges, respectively.

Discussion

Age and growth

This study is the first to report otolith-derived age estimates for pinfish. Hansen (1970) reported scale-derived age estimates for pinfish from a Florida Panhandle estuary. In the current study, annuli were identified and counted on whole otoliths and were then identified and counted on thin sections. The high initial agreement (89.6%) between the age determinations of the author and a second reader suggests a high degree of precision can be attained without sectioning the otolith. Given the high degree of error generally associated with estimating ages of fish from their scales (Jearld, 1983; Beamish and McFarlane, 1987), I believe that age estimations made from pinfish otoliths are far more likely to be accurate.

Deposition of opaque material in the sagittal otoliths of pinfish occurs over a protracted late-winter to early-spring period and indirectly validates the formation of annuli in

Table 5

Results of the generalized linear model analysis of ln (x+1) pinfish catches (in number per nmi^2) from the baitfish cruises in the Gulf of Mexico, 1994–97. ***=$P \leq 0.001$.

Source	df	MS	F	r^2
Model	7	79.9	16.1***	0.680
Year	3	25.5	5.1***	
Depth	1	389.3	78.4***	
Year × depth	3	31.3	6.3***	
Error	53	5.0		
Corrected total	60	13.7		

pinfish. Similarly, Hansen (1970) found that annuli on scales are generally formed once a year, in April.

The maximum age of pinfish determined in this study was 7 years, which exceeded the maximum age of 2 years reported by Hansen (1970). The difference in maximum age is probably due to Hansen's inadequate sampling of the entire size range of pinfish in Pensacola Bay—he collected pinfish at only two stations using a single, selective trawl. In addition, Hansen's use of scales as the primary aging structure may have contributed to the underestimate of the maximum age of pinfish (Beamish and McFarlane, 1987). In contrast, pinfish collected in this study were sampled from numerous locations in Tampa Bay and adjacent Gulf waters with multiple types of gears that had various mesh sizes, and otoliths, which are more reliable aging structures than scales (Beamish and McFarlane, 1987), were used for age determination. Coincidentally, Caldwell (1957) projected from the growth rates of age-1 pinfish that a 328-mm-SL pinfish may have been as old as 7 years; my results provide direct evidence that supports his estimate.

Reproduction, sex ratios, and maturity

The monthly changes in GSIs show that pinfish are late-autumn to early-spring spawners in Tampa Bay and adjacent Gulf of Mexico waters; this conclusion was also reported by Darcy (1985) and Cody and Bortone (1992). Pinfish spawning is suspected to occur in offshore oceanic waters (Hansen, 1970; Darcy, 1985); however, the high GSIs of pinfish collected in Tampa Bay and the occurrences of several of these pinfish with late-developing gonads in waters about 3–6 km into the bay during October–December suggest that some spawning activity may occur in this estuary. This is not surprising because most studies that have examined gonadal activity in pinfish have used samples only from offshore waters (Franks et al., 1972; Stott et al., 1980, 1981), did not use gear with various mesh sizes to adequately sample the entire size range of pinfish found in estuaries (Caldwell, 1957; Hansen, 1970), or did not compare data on an estuary-offshore basis (Cody and Bortone, 1992).

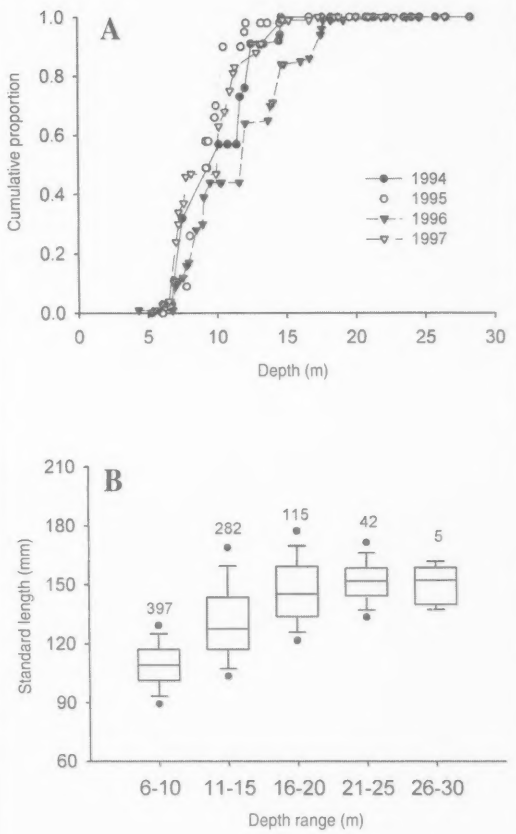

Figure 7

Plots of (**A**) cumulative catch versus depth by year and (**B**) size frequency of pinfish by depth range from the baitfish trawl survey, 1994–97. In B, the lower and upper dots represent the 5th and 95th percentiles of the length distribution, the whiskers represent the 10th and 90th percentiles, the box represents the 25th and 75th percentiles, and the horizontal line represents the median length.

Length-weight relationships

The length-weight relationships were affected by gonadal maturation. During the September–February period, gonad weight of both sexes increased, which resulted in a standard-length to total-body-weight relationship that was higher than it was in March–August period. Differences in predicted total weight at length were 2–8% between the September–February and March–August periods and illustrate the effect of maturation on these relationships. The slopes of the length-weight relationships from both periods (3.03–3.11) were higher than the slopes of length on weight relationships (2.91 and 2.90, respectively) developed by Caldwell (1957) and Cameron (1969).

Mortality

This study is the first to report total instantaneous mortality (Z) rates (0.88–1.08) for pinfish older than young-of-the-year. It is difficult to conclude whether the mortality rate in Tampa Bay is really higher than that in the Gulf. The small mesh characteristics of the sampling gear, the restricted spatial coverage of sampling from Tampa Bay to the shallows of the estuary where young pinfish dominate (most gears were employed in waters <3 m), or the migration of pinfish from estuaries to offshore waters to spawn may have contributed to the older (>age 1) fish being underrepresented in the sampling of bay waters (Hansen, 1970; Darcy, 1985; Nelson, 1998). By assuming that pinfish are fully recruited at age 2 (Table 4), I estimated that Z from data for both areas combined is probably more realistic because the numerical proportions of pinfish ages 2 and older in Tampa Bay were nearly identical to the numerical proportions of pinfish age 2 and older from the Gulf of Mexico. The estimate of Z from data for both areas combined (0.90/yr) was close to the natural mortality estimate of 0.78/yr, suggesting that the portion of annual mortality attributed to fisher activity, calculated by $(Z–M)/Z$, is low [13%].

Distribution

Darovec (1995), Franks et al. (1972), and Darcy and Gutherz (1984) reported that pinfish from the Gulf of Mexico occurred in trawls to depths between 73 m and 93 m. However, most pinfish captured in Gulf waters off west-central Florida were captured from depths <19 m (Darovec, 1995). The results from the baitfish survey were very similar in that most pinfish (95%) were caught in waters <17 m, but the abundance-depth relationship varied between years, and larger pinfish were generally associated with greater depths. The propensity of pinfish to limit their depth distribution and alter their size distribution with depth is probably due to the distribution of their epibenthic prey (Stoner, 1980; Nelson and Bortone, 1996), the distribution of their predators, and (because pinfish are visual feeders) reduced light intensity with depth (Kjelson and Johnson, 1976; Luczkovich, 1988).

In summary, ages determined from whole otoliths ranged from 0 to 7 years, and von Bertalanffy growth model parameters for all aged fish were L_∞=219.9 mm SL, k =0.33/yr, and t_0 =–1.10 years. High gonadosomatic indices during October–December indicated that some spawning may occur in Tampa Bay. Estimated lengths at 50% maturity were 132 mm SL for males and 131 mm SL for females. Total instantaneous mortality rates from the Chapman-Robson estimator ranged from 0.88 to 1.08/yr, and natural mortality based on Pauly's (1980) equation was 0.78/yr. Catch rates of pinfish were related to depth in the Gulf of Mexico.

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Recovery of the Gulf of Maine–Georges Bank Atlantic herring (*Clupea harengus*) complex: perspectives based on bottom trawl survey data

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Abstract–NMFS bottom trawl survey data were used to describe changes in distribution, abundance, and rates of population change occurring in the Gulf of Maine–Georges Bank herring (*Clupea harengus*) complex during 1963–98. Herring in the region have fully recovered following severe overfishing during the 1960s and 1970s. Three distinct, but seasonally intermingling components from the Gulf of Maine, Nantucket Shoals (Great South Channel area), and Georges Bank appear to compose the herring resource in the region. Distribution ranges contracted as herring biomass declined in the late 1970s and then the range expanded in the 1990s as herring increased. Analysis of research survey data suggest that herring are currently at high levels of abundance and biomass. All three components of the stock complex, including the Georges Bank component, have recovered to pre-1960s abundance. Survey data support the theory that herring recolonized the Georges Bank region in stages from adjacent components during the late 1980s, most likely from herring spawning in the Gulf of Maine.

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The Atlantic herring (*Clupea harengus*) resource in the Northwest Atlantic has been an important source of food and commerce for nearly four centuries (Anthony and Waring, 1980). Simple wier fisheries with relatively low landings began in the 1600s in both the United States and Canada but evolved into much larger operations, and landings increased. The most important early fishery for herring in the United States developed in the late 1800s, resulting in the building of numerous sardine canning plants, with annual landings eventually ranging from 60,000 metric tons (t) to 100,000 t by the early to mid 1900s (Anthony and Waring, 1980). An important weir fishery developed in New Brunswick during the 1950s and provided fish for canning operations in the region. Both the U.S. and Canadian fisheries initially focused on juvenile fish; fisheries for adults developed only when the abundance of juveniles (available to fixed gear) declined in the early 1960s (Anthony and Waring, 1980).

In the early 1960s Atlantic herring on Georges Bank became the focus of a major fishery by gill-net vessels from the former Soviet Union (Hennemuth and Rockwell, 1987). By the mid 1960s distant-water herring fisheries had developed in the Gulf of St Lawrence, on the Scotian Shelf, on Georges Bank, and on Jeffreys Ledge (Fig. 1) (Anthony and Waring, 1980). Landings of herring from the Gulf of St Lawrence to Georges Bank peaked at over 900,000 t in 1968, declining steadily thereafter (Anthony and Waring, 1980).

The Georges Bank herring fishery (combined Nantucket Shoals and Georges Bank region) began in 1961 and increased rapidly to a peak of 373,000 t in 1968 (Figs. 1 and 2). During the early 1970s, landings steadily declined and in 1977 the herring fishery on Georges Bank collapsed (low landings and abundance) (Fig. 2) (Anthony and Waring, 1980; Tupper et al.[1]). During the same period, landings in the Gulf of Maine fishery ranged from 35,000 to 82,000 t (Fig. 2).

Stock assessments prepared by the International Commission for Northwest Atlantic Fisheries (ICNAF) for Georges Bank herring (combined Nantucket Shoals and Georges Bank) began in the late 1960s, and annual total allowable catch quotas (TAC) were established in 1972. Annual assessments were conducted by using virtual population analysis (VPA) and results from these assessments revealed that the Georges Bank component peaked in abundance in 1967 and rapidly declined thereafter (Anthony and Waring, 1980). These findings were confirmed by larval herring surveys conducted during the 1970s and 1980s, where a general decline in larval abundance in the region was noted during 1975–78 and the complete absence of herring larvae in the Georges Bank-Nantucket

[1] Tupper, M. H., V. C. Anthony, S. B. Chenoweth, and H. A. MacCluen. 1998. Biology and assessment of Gulf of Maine herring stocks, 104 p. Gulf of Maine Aquarium, PO Box 7549, Portland, ME 04112.

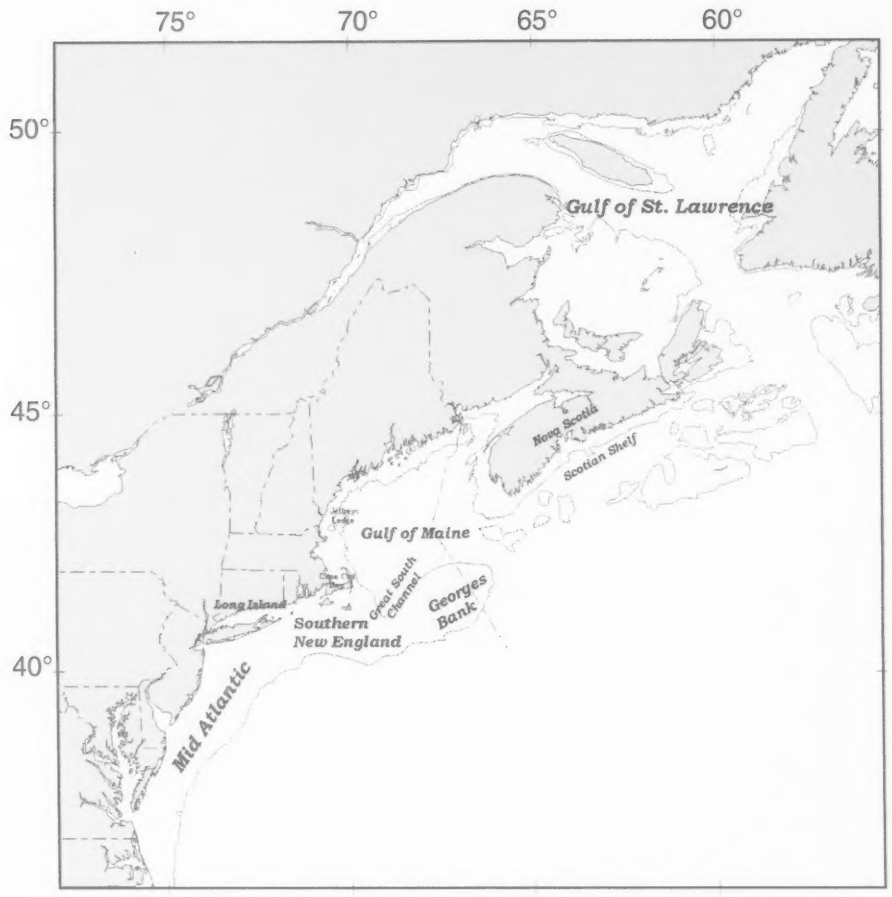


Figure 1

Regional map of the Mid-Atlantic, New England, and Canada area showing states, the providence of Nova Scotia, offshore place names, and the 100-m depth contour.

Shoals region during 1979–84 (Lough et al., 1985; Smith and Morse, 1993).

Presently pelagic fishes such as Atlantic herring and mackerel (*Scomber scombrus*) have recovered to historic high abundances (Clark, 1998). Atlantic herring have recovered to pre-1960s biomass and abundance and are now becoming the subject of renewed interest by fleets from the United States and Canada (Clark, 1998; NEFSC[2]). During a recent survey (spring 1999), herring were caught in 47% of the standardized tows and represented one of the top five species in terms of abundance and biomass (NEFSC[3]).

The presence and increase of spawning fish and larvae in historically important areas of Nantucket Shoals (Great South Channel area), Georges Bank, and along the coast of Maine have been documented ((Zinkevich, 1967; Stephenson and Kornfield, 1990; Smith and Morse, 1993; Stevenson[4]).

The purpose of this paper is to describe the magnitude of the decline and recovery of the herring complex in the Gulf of Maine–Georges Bank region and the chronology of

[2] NEFSC (Northeast Fisheries Science Center). 1998. Atlantic herring: report of the 27th Northeast regional stock assessment workshop (27th SAW). Stock Assessment Review Committee (SARC) consensus summary of assessments, 27 p. Northeast Fisheries Science Center, Woods Hole, MA 02543.

[3] NEFSC (Northeast Fisheries Science Center). 1999. Fisherman's report: bottom trawl survey. Woods Hole Laboratory, National Marine Fisheries Service, March 1–April 22, 1999, 20 p. Northeast Fisheries Science Center, Woods Hole, MA 02543.

[4] Stevensen, D. K. 1989. Spawning locations and times for Atlantic herring on the Maine Coast. Maine Department of Marine Resources Research Reference Document 89/5, 24 p. Maine Department of Marine Resources, Boothbay Harbor, ME 04575.

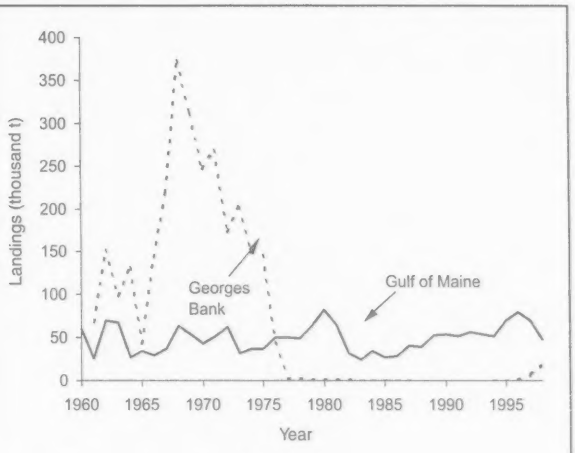


Figure 2

Landings of Atlantic herring (thousands of t) from the Gulf of Maine and Georges Bank, 1960–98.

the differential recovery by area by using NEFSC bottom trawl data from 1963 to 1998. We also wanted to examine two theories regarding the recovery of Georges Bank herring: 1) that it was due to a resurgence of extant spawners (Stephenson and Kornfield, 1990) or 2) that is was due to recolonization from adjacent components of the complex (Smith and Morse, 1993).

Methods

Details of the statistical design, areal coverage, standardization methods, gear type, and species catchability in the NEFSC bottom trawl surveys are provided in Grosslein (1969); Azarovitz (1981); Byrne et al. (1981), and a NEFSC report (NEFSC, 1988). Briefly, the surveys are based on a stratified random research design that covers the region from Cape Hatteras to the Scotian Shelf at depths between 27 and 200 m (15 to >100 fathoms), each spring and autumn.

We used data from spring (1968–98) and autumn (1963–98) bottom trawl surveys to produce indices of abundance, and plot distribution patterns for the Gulf of Maine–Georges Bank Atlantic herring complex. For spring, we used the same strata set (strata 1–30, 33–40, and 61–76) (Fig. 3) as used in the assessment of the herring complex (NEFSC[2]). We produced indices of total abundance (swept area numbers [millions]) to follow changes in the stock complex over time, assuming that a standardized survey tow covers 0.1 nmi and that all herring are available to the gear.

For autumn we used a smaller strata set (1–30, 33–40) (Fig. 3) to generate indices of abundance (area-swept numbers) because herring are seldom found south and west of Long Island during this season (NEFSC[2]). Changes in abundance by subregion (reflecting abundance trends by spawning components) were assessed by using indices for the Gulf of Maine (strata 26–28, 37–40), Nantucket Shoals (Great South Channel area) (strata 9–11, 23–25), and Georges Bank (strata 13–14, 16–17, 19–22, 29–30) (Fig. 3).

We produced box plots that represent the median survey catch location aggregated over a latitudinal gradient (35–45°N latitude) collapsed over the entire east-west longitude of the region. We repeated the same procedure for the longitudinal gradient (64–76°W longitude). These plots show the median, inter quartiles (25% and 75%), whiskers (1.5 times the absolute value of the interquartile range) and outliers of the data. We also constructed maps of spring survey catch locations for 1970, 1975, 1980, 1985, 1990, and 1995 to show trends in herring distribution and abundance over the time period. Changes in distribution and abundance during autumn 1963–98 are depicted in plots of Atlantic herring catch locations for 1965, 1970, 1975, 1980, 1985, 1990, and 1995.

We also produced box plots of bottom temperature for the sites where herring were captured during both seasons. For spring and autumn, we also plotted the proportion of survey tows with catches of Atlantic herring as a measure of how often surveys encountered Atlantic herring over the time series. We used LOWESS (locally weighted regression smoothing) (Cleveland, 1979) to make the temporal trends in both of these time series easier to follow.

Results

Atlantic herring abundance indices from spring surveys changed markedly during 1968–98 (Fig. 4A). A period of relatively high abundance (area swept, millions of fish), in

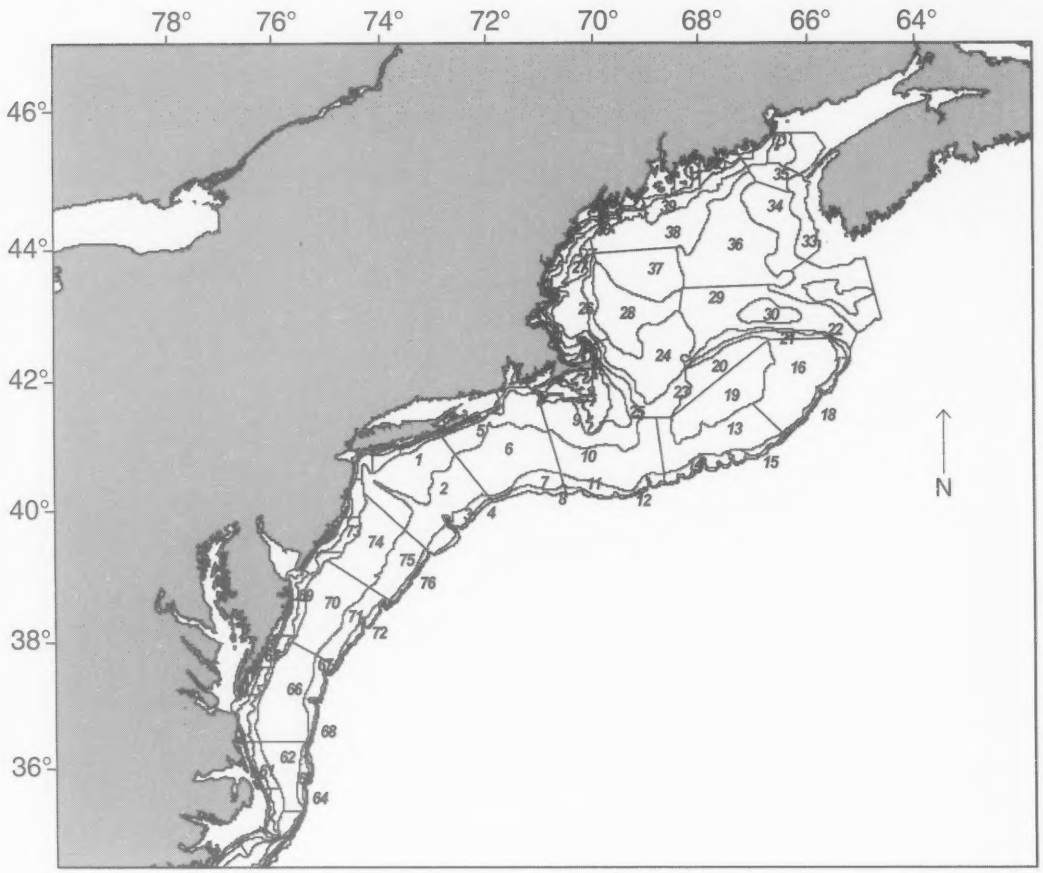


Figure 3

Survey strata used in the Northeast Fisheries Science Center research bottom trawl surveys for the region from Cape Hatteras, NC, to Nova Scotia, Canada.

the late 1960s was followed by a low abundance from 1971 to 1985. After 1985, abundance indices increased steadily to values that were 2–3 times larger (1993, 1996–98) than those at the beginning of the time series (Fig. 4A). Atlantic herring abundance was six times higher during 1992–98 than during 1968–75.

Herring spawn between mid-September and mid-October, and the timing is dependent on location and year. The NEFSC autumn research survey is usually conducted just after the spawning season for Atlantic herring, but this survey is a useful indicator of the abundance of spawners in the various component areas. Herring abundance in the autumn surveys was low (range 2.5–17.7 million fish) during 1963–67, very low from 1968–1986 (range 0.0–4.4 million fish), and much higher since 1987 (range 45.6–604.2 million fish) (Fig. 4B).

The herring complex occupied a consistently wider latitudinal range in the spring during the late 1980s and 1990s than in prior years. The complex was centered between 39°–41°N latitude during 1968–70 and then gradually shifted northwards (Fig. 5A). During 1982–84, the median latitude of the complex had moved north to 42° (north of Cape Cod); by 1984, the distribution of the stock complex was confined between 40°30′–44°10′N latitude, about a 50% decrease in latitudinal range as compared to 1968 (Fig. 5A). As abundance increased in the late 1980s, the center of the spring distribution of Atlantic herring moved southwards and the range extended; since 1989 the medial latitudinal position of the complex has remained at 41°N (Fig. 5A)

Major shifts in the longitudinal position of the complex have also occurred. During 1968–70, herring were generally west of 70°W longitude (Fig. 5B). Subsequently (through 1986) the complex shifted farther to the east. As abundance increased, in the late 1980s, the longitudinal center of the complex moved westward remaining at about 70°W longitude during 1989–98. During this time period, the east-west extent of the complex expanded greatly (Fig. 5B).

The median, interquartile range, and overall range in latitude of the herring complex in autumn is character-

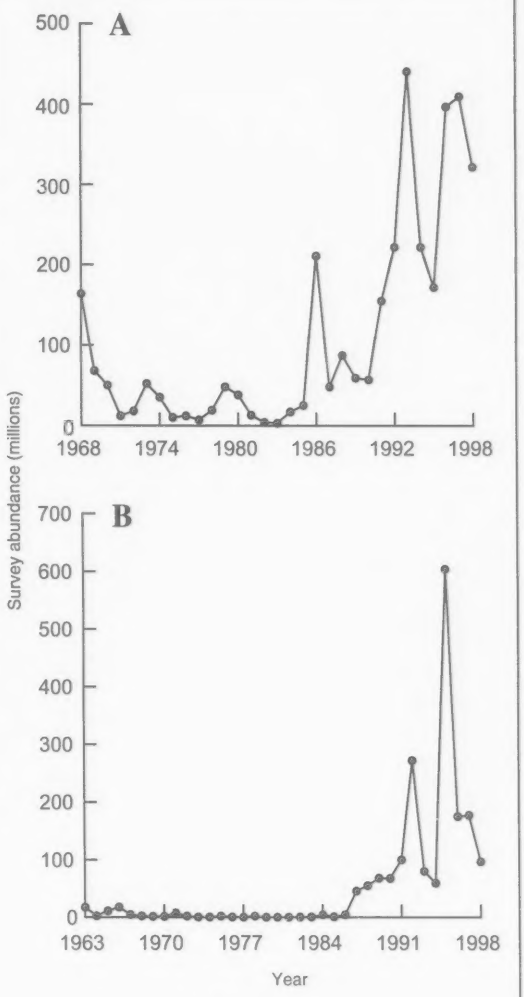


Figure 4

Abundance indices (swept area, millions of fish) of Atlantic herring from (**A**) spring bottom trawl surveys during 1968–98 and (**B**) autumn bottom trawl surveys during 1963–98.

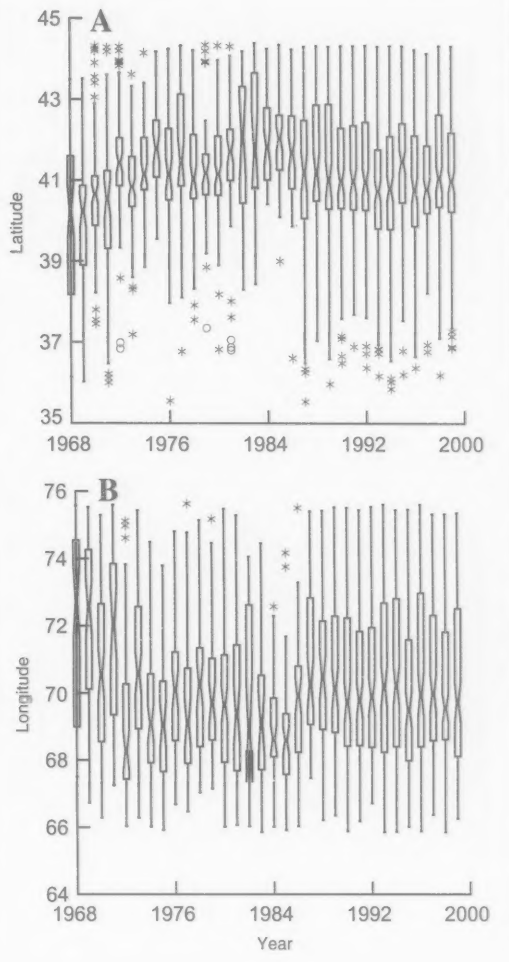


Figure 5

Median (notch), interquartile range, whiskers (±1.5 times the absolute value of the interquartile range), values outside the whiskers (*), and far outside the whiskers (o) of the (**A**) latitude and (**B**) longitude of positive catches of Atlantic herring from the spring NEFSC bottom trawl survey during 1968–98.

ized by rapid changes and a general movement to the north during 1963–75 (Fig. 6A). During 1963–64, the stock complex was centered around 42°, moved a full degree to the south by 1967, and then shifted north to almost 43° by 1975. Survey abundance was so low during 1976–81 that any trends in median latitude were obscured (Fig. 6A). As the stock recovered, median latitude became stable, ranging between about 42°00′ and 42°30′.

The median longitude of the complex hovered around 68°15′–68°45′ during 1963–72, then shifted to the west of 69° during 1973–86 (Fig. 6B). When recovery began, the median longitude of the complex moved slightly to the east of 69°, stabilized between 69°30′ and 69°50′ during 1991–95, and moved farther east during 1996–98 to about 68°35′ (Fig. 6B).

Since 1968, median bottom water temperatures for the entire continental shelf during spring have fluctuated between 5° and 7.5°C, with individual bottom locations ranging between 1° and 14°C and a few values falling outside this range (NMFS[5]). Herring maintained their pref-

[5] NMFS (National Marine Fisheries Service). 2001. Unpubl. data. Northeast Fisheries Science Center, Woods Hole, MA 02543.

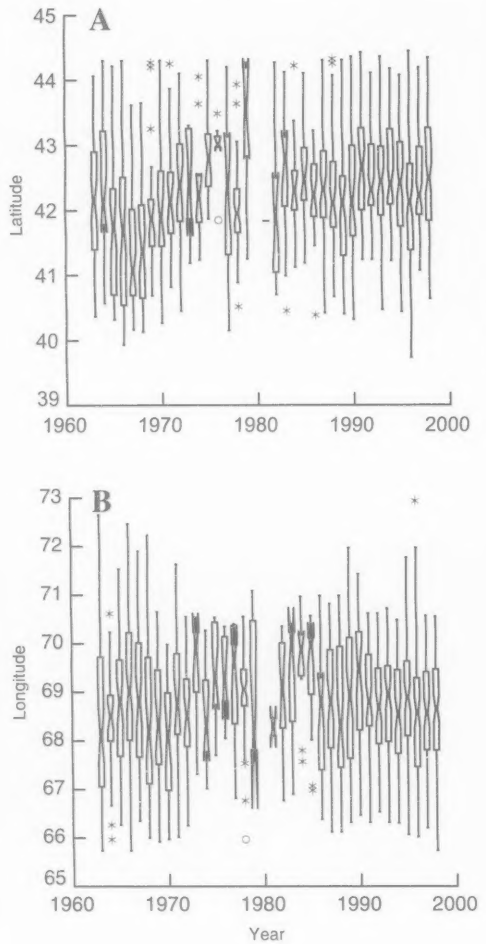


Figure 6

Median (notch), interquartile range, whiskers (±1.5 times the absolute value of the interquartile range), values outside the whiskers (*), and far outside the whiskers (o) of the (**A**) latitude and (**B**) longitude of positive catches of Atlantic herring from the autumn NEFSC bottom trawl survey during 1963–98.

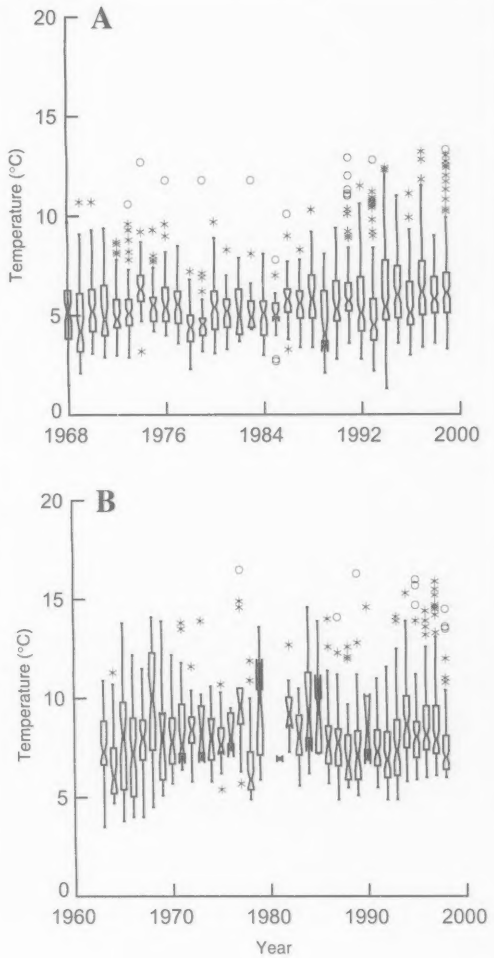


Figure 7

Median (notch), interquartile range, whiskers (±1.5 times the absolute value of the interquartile range), values outside the whiskers (*), and far outside the whiskers (o), of the bottom temperature of positive catches of Atlantic herring from the (**A**) spring NEFSC bottom trawl survey during 1968–98 and (**B**) autumn NEFSC bottom trawl survey during 1963–98.

erence for water temperatures that were cooler than the annual shelf-wide ranges; most herring were caught at bottom temperatures around 5°C during 1968–94 and at about 6°C thereafter (Fig. 7A). During 1972–91, the interquartile range in capture temperature was very narrow, about 1–2°C, expanding afterwards to 2–3°C (Fig. 7A). The overall range in capture temperatures increased greatly in the 1990s.

The median bottom water temperature for the continental shelf during autumn 1963–98 fluctuated between 8° and 12°C, and ranged between 3° and 25°C with a few higher observations (NMFS[5]). Herring were generally captured in the autumn surveys at bottom water temperatures around 8°C during 1963–76 and at about 7–8°C from 1983 to 1998 (Fig. 7B). The interquartile range in capture temperature was about 2–4°C (Fig. 7B), again much cooler than the shelf-wide ranges.

The proportional number of locations where Atlantic herring were captured during spring surveys declined

from 0.30 in 1968 to 0.09 in 1982 (Fig. 8A). During 1983–93, herring were captured in an increasing proportion of survey hauls; by the 1990s, the herring proportion in all survey tows was over 0.60 (Fig. 8A). Autumn surveys during the 1960s and 1970s also showed a declining trend in the proportion of stations containing herring. This decline was even more pronounced than in spring, with the proportion of herring at less than 0.05 of the sample sites during 1979–81 (Fig. 8B). This trend began to change in 1982 and by the 1990s the proportion of tows with herring was well over 0.40 (Fig. 8B).

Spring distribution maps from selected years (1970–95) show that significant changes in herring distribution occurred during 1968–98. In 1970 herring were encountered at 74 sites in the central Gulf of Maine (GOM), on southern Georges Bank (GB), and across the continental shelf from south of Nantucket to Chesapeake Bay (Fig. 9). During 1975, fewer sampling locations (39 sites) had herring and the distribution was constricted. The complex was confined to a few areas in the central GOM, on southern GB, south of Cape Cod, and off of Long Island (Fig. 9). In 1980, fish were encountered (89 sites) along eastern GB and found across western-southern GB to south of Long Island. During 1985, the spring distribution (48 sites) was more restricted than in 1980. By 1990 Atlantic herring were found at 101 sites throughout the GOM, western and southern GB, and across the shelf from Cape Cod to Chesapeake Bay. In 1995, herring were even more widely dispersed (108 sites) across the continental shelf.

Abundance of herring from these selected spring research survey years reflect the general decline in the stock in the late 1970s and recovery to much higher levels in the late 1990s (Fig. 9). In 1970, herring were abundant over the entire continental shelf from Nantucket to Chesapeake Bay with the highest abundance off Long Island and New Jersey (Fig. 9). During the late 1970s, through the mid 1980s, herring were less abundant and the largest catches (101–500 fish per station) were generally taken south of Cape Cod (Fig. 9). By the 1990s, herring were abundant over a wider area and catches in the 101–500 fish-per-tow range were common.

Maps of autumn survey catch locations depict significant spatial changes in herring distribution during the past 30 years (Fig. 10). In 1965 postspawning fish were located (47 sites) in the central GOM, on Jeffreys Ledge, Nantucket Shoals, and the shelf-slope break along western to northern GB (Fig. 10). In 1970 herring were caught at 25 sites (mostly in the GOM and on eastern GB), in 1975 at only 18 sites, and in 1980 at only one location (along the coast of Maine). The number of capture sites increased in 1985 (17) when herring were found primarily in the Stellwagen Bank-Jeffreys Ledge region, and at a few sites on Georges Bank (Fig. 10). In 1990, herring were widely dispersed (31 sites) along the coast of Maine, Jeffreys Ledge, and Nantucket shoals, and in 1995 herring were dispersed throughout the entire region (75 sites) (Fig. 10).

In the early part of the autumn survey time series, herring were widely dispersed, but not very abundant. In 1965, only a few tows had catches greater than 50 fish (Fig. 10). During 1970–85 very few herring were taken and most tows represented only single fish (Fig. 10). By 1990 a general recovery was apparent and catches of 50+ fish per station were common. Atlantic herring were again abundant along the coast of Maine, on Jeffreys Ledge, and in the Great South Channel area (Fig.10). In 1995, herring were abundant over the entire Gulf of Maine–Georges Bank region.

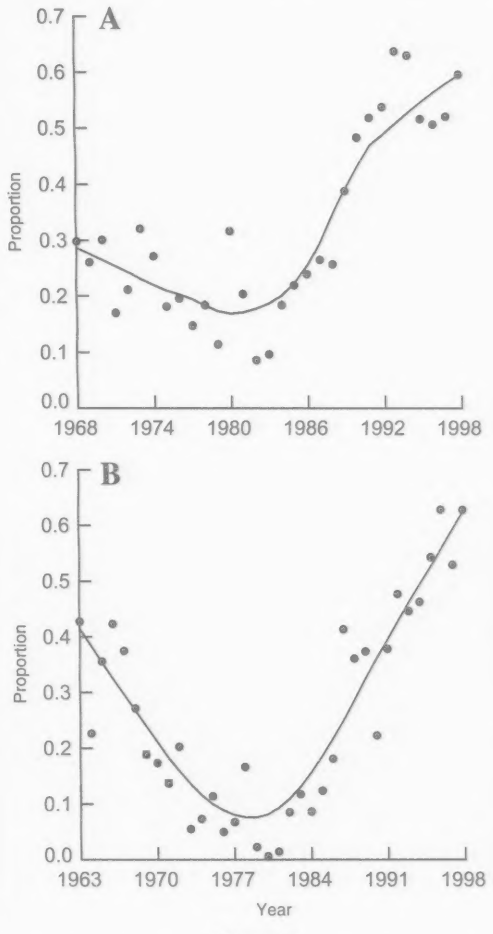


Figure 8

Proportion of survey tows with positive occurrences of Atlantic herring with a LOWESS curve for the data from (**A**) spring bottom trawl surveys during 1968–98 and (**B**) autumn bottom trawl surveys during 1963–98.

Survey abundance indices of herring in the Gulf of Maine, on Nantucket Shoals, and on Georges Bank, increased greatly since the mid 1980s, but at different rates (Fig.11). Increases in the GOM (range 2.8–85.9 million fish, 1987–98) and GB (range 2.1–120 million fish, 1991–98) regions appeared to be about equal in magnitude although the recovery in the GOM began earlier than on GB (Fig.

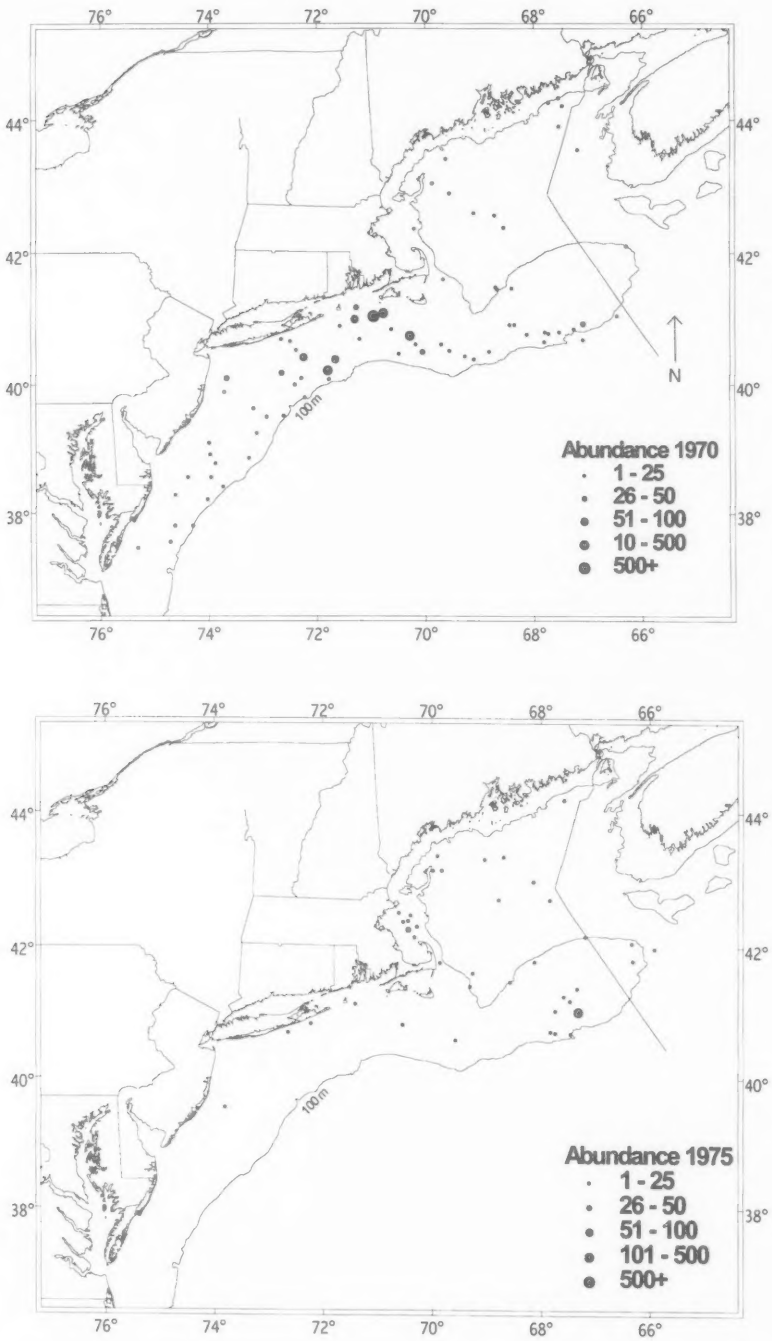
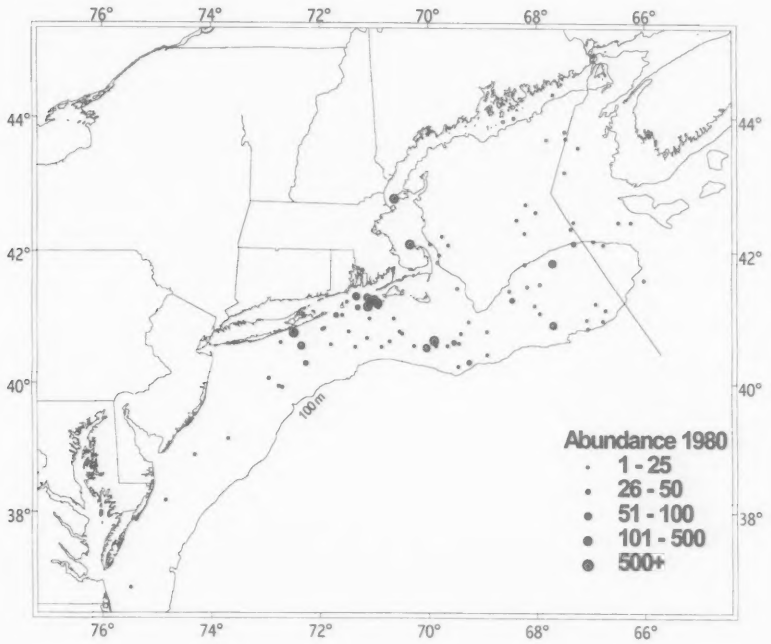
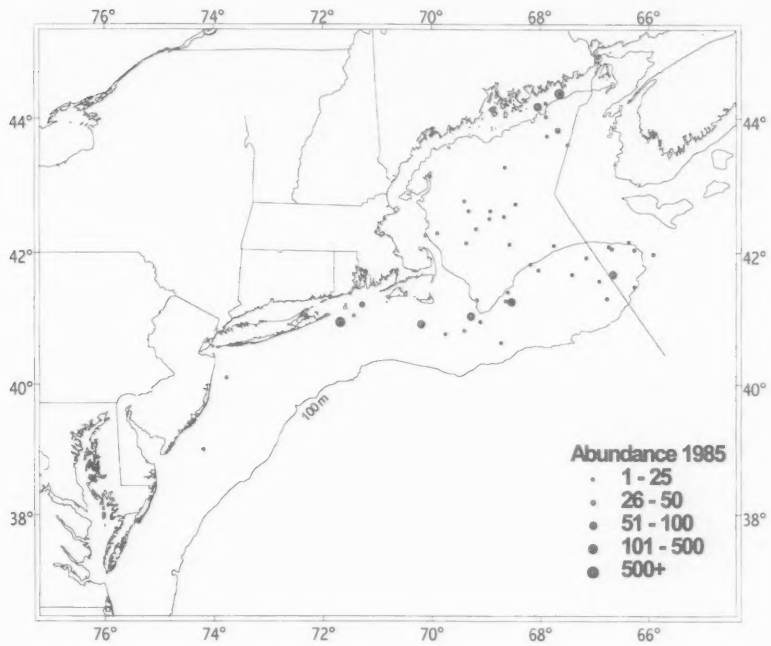


Figure 9

Catch locations and abundance (number of fish per station) for Atlantic herring for selected years (1970, 1975, 1980, 1985, 1990, 1995) from spring bottom trawl surveys conducted during 1968–98.





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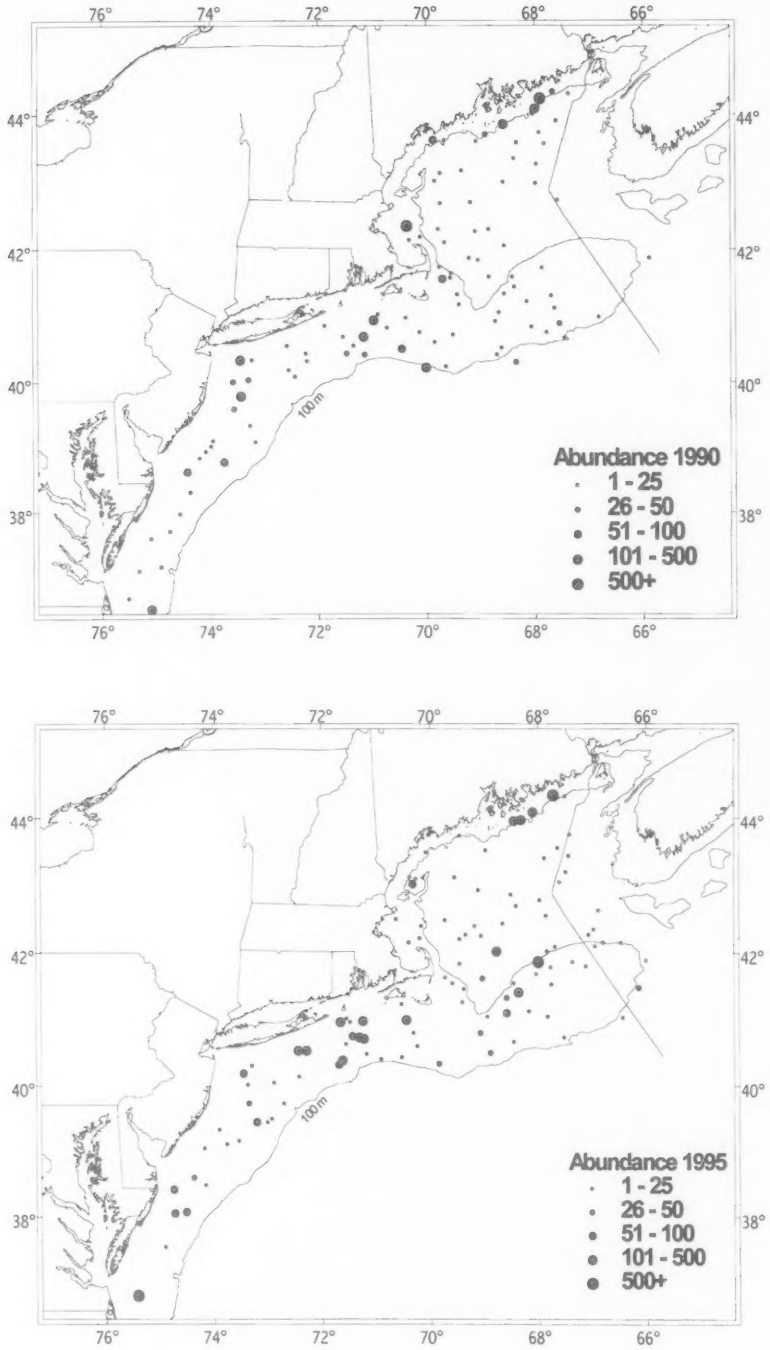

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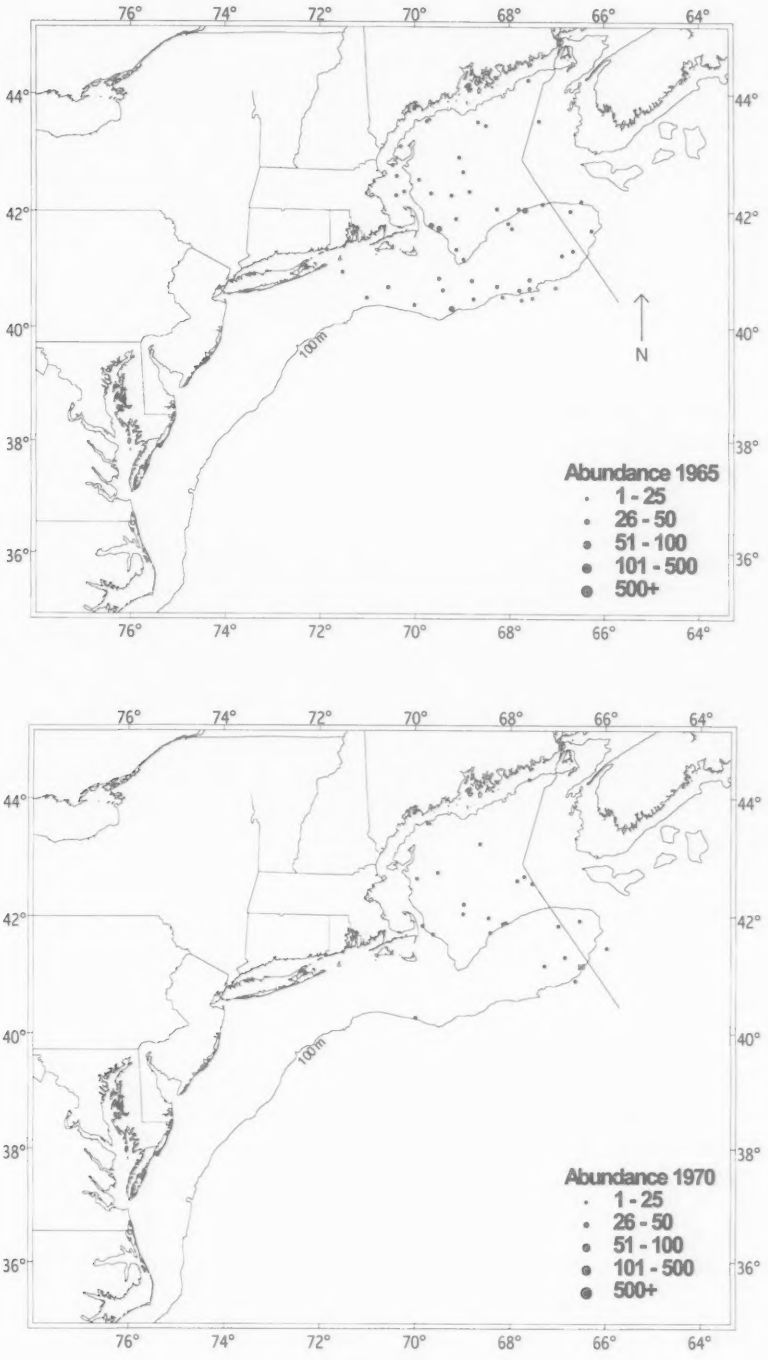
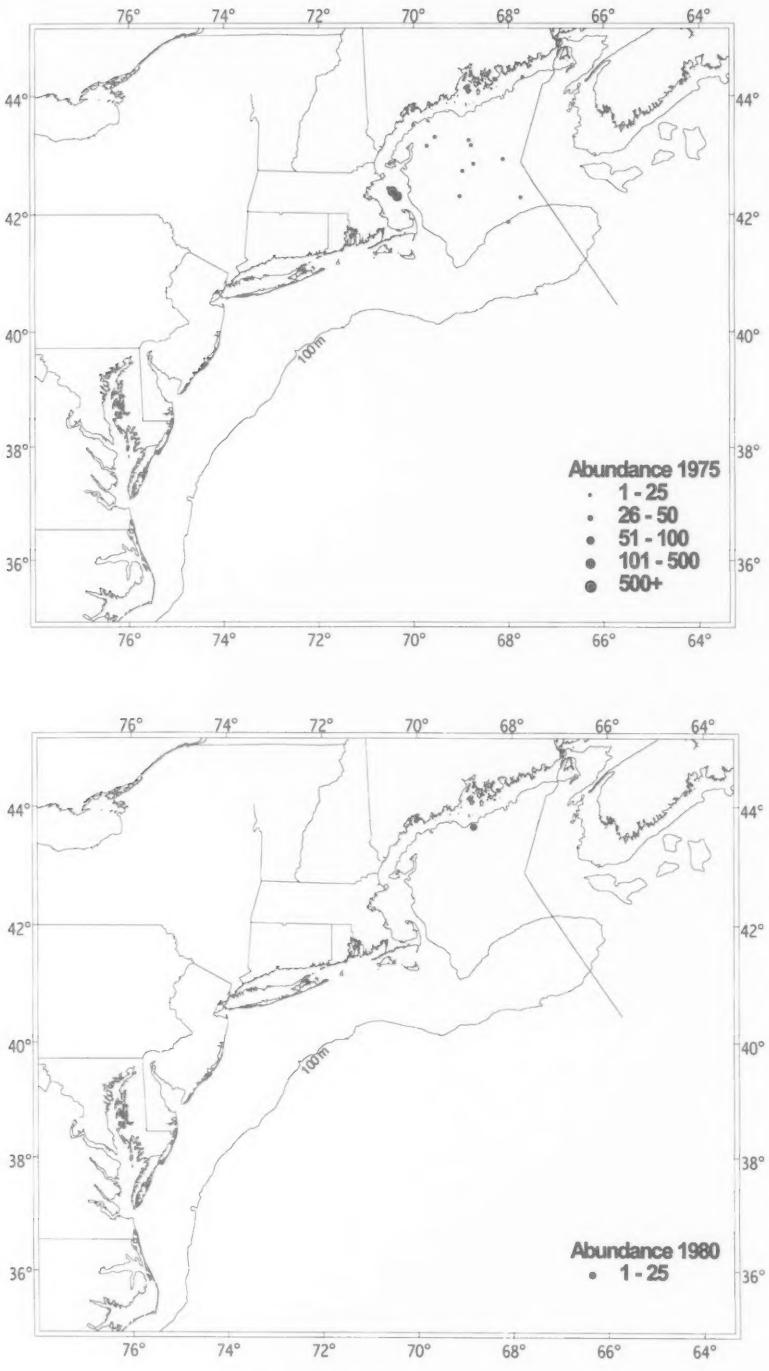


Figure 10

Catch locations and abundance (number of fish per station) for Atlantic herring for selected years (1965, 1970, 1975, 1980, 1985, 1990, 1995) from autumn bottom trawl surveys conducted during 1963–98.



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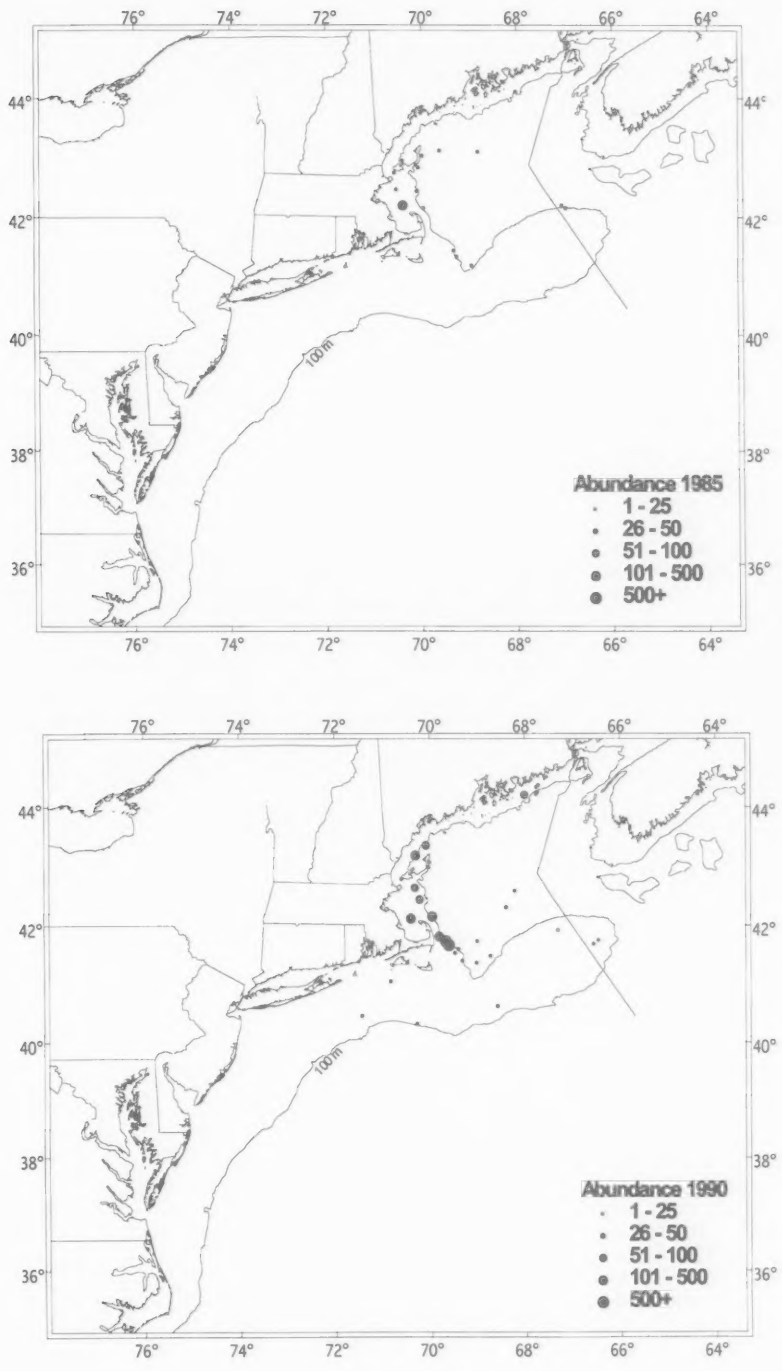

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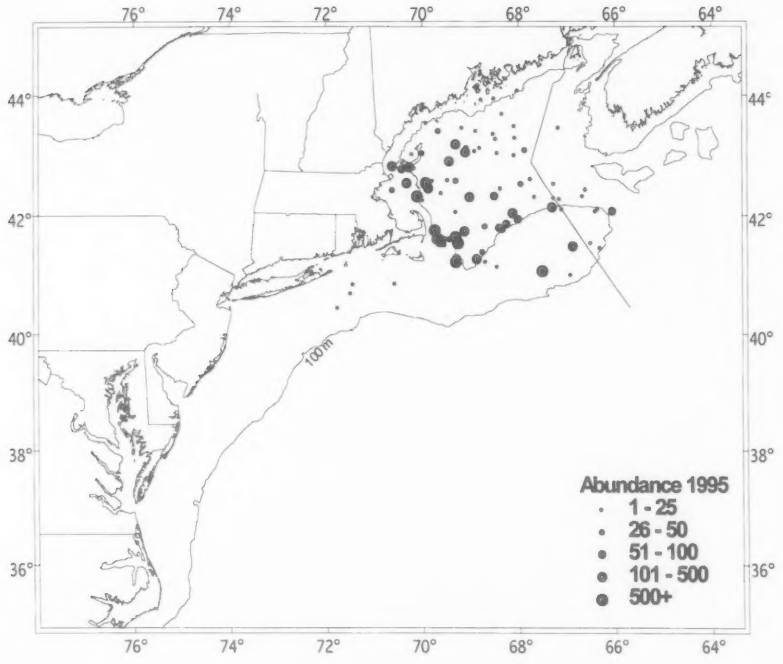

Figure 10 (continued)

11). The recovery in the Gulf of Maine started in 1984 and continued through to 1998 (Fig. 11A). The largest overall increase in abundance has occurred in the Nantucket Shoals region (range 28.8–398.3 million fish) (Fig. 11B). Similarly, after a long hiatus from 1963–1986, this stock component increased considerably during 1987–98. The Georges Bank component was the last to recover, with significant increases in abundance beginning in 1992 (Fig. 11C).

Discussion

Atlantic herring are currently abundant in the Gulf of Maine–Georges Bank region as evidenced by research survey results and recent stock assessments (NEFSC[2]). This resource was heavily exploited during 1961–76 by distant-water fishing vessels with catches that were not sustainable, resulting in the collapse of the Georges Bank component in 1977. The causes of this collapse have been ascribed to excessive fishing mortality and concentration of effort on spawning areas (Anthony and Waring, 1980). ICNAF routinely set total allowable catches (TACs) in excess of scientific recommendations and these TACs were often exceeded (Anthony and Waring, 1980). Spawning concentrations were heavily fished, and egg and larval production declined steadily, followed by the complete absence of larvae on Georges Bank for an entire decade (Anthony and Waring, 1980; Lough et al., 1985; Smith and Morse, 1993).

Full recovery of the Atlantic herring resource has required almost two decades (NEFSC[2]). Spawning area closures and restrictions in the Gulf of Maine beginning in the 1980s may have been influential, but the relative impact of these indirect measures cannot be assessed (Stevenson[4]). During 1978–94 there were almost no offshore landings and abundance and biomass for the GB component improved steadily (NEFSC[2]).

The distribution range of the herring complex was greatly reduced after each of the three stock components were heavily fished; the extent of the spring distribution was much reduced by the early 1980s and autumn spawning activity was confined to the western Gulf of Maine. The relative encounter rate in both research surveys, as measured by the proportion of tows with herring, also declined during this period. As the complex began to recover, its range extended and the proportion of survey tows with herring increased dramatically. The complex was more widely dispersed by the mid 1990s with the recovery of all three components to, or above, historic abundance and biomass (NEFSC[2]).

Murawski (1993) found that temperature is a very important factor in determining the distribution of pelagic fishes, particularly Atlantic herring. Herring appear to have maintained a preferred thermal regime despite elevated and variable overall shelf temperatures in spring and autumn, and large changes in abundance. The ±5°C median spring temperature for 1968–94 from our study is in agreement with the average of 4.8°C from Murawski (1993). After the complex recovered, the median spring bottom temperature increased slightly to about 6°, probably indicative of the much broader range of the complex. Murawski (1993) calculated an autumn average of 8.5° for Atlantic herring and the median from the current study was 7–8°. This autumn preference reflects the distribu-

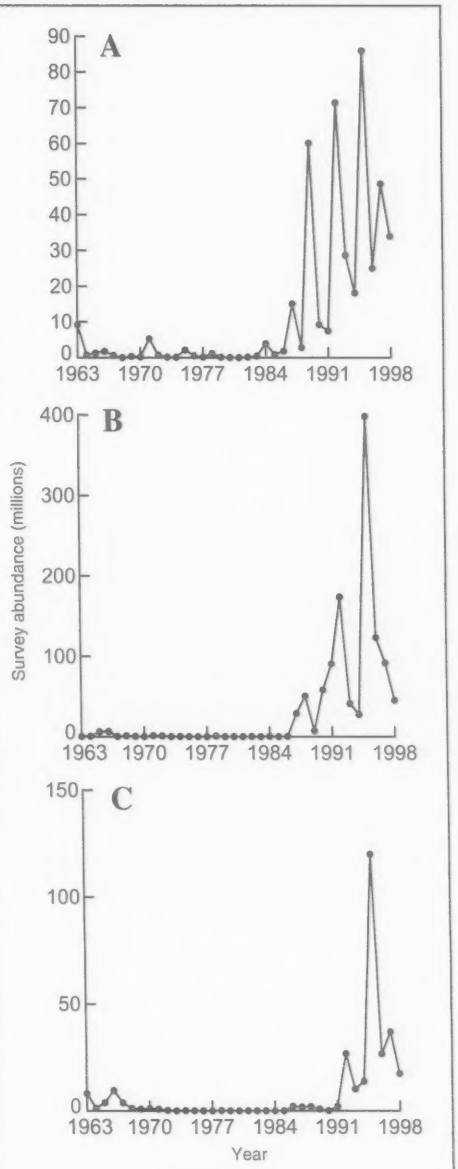

Figure 11

Abundance (swept area, millions of fish) of Atlantic herring from (**A**) the Gulf of Maine, (**B**) Nantucket Shoals, and (**C**) Georges Bank from autumn bottom trawl surveys during 1963–98.

tion of postspawning fish in the cooler waters of the Gulf of Maine and Northern Georges Bank. Although thermal conditions play a major role in the zoogeography of fishes, the influence of abundance was probably overwhelming in producing the recovery of the historic range in distribution observed in the Atlantic herring complex.

Several independent sources of information suggest that the recovery of this stock occurred in a stepwise manner with the Gulf of Maine component recovering first, followed by the Nantucket Shoals component, and finally the Georges Bank component. The autumn bottom trawl survey data showed an improved trend in the Gulf of Maine in 1984, the Nantucket Shoals component in 1987, and Georges Bank in 1992. Larval surveys conducted during 1971–90 showed a progression of larval abundance from the Cape Cod Bay-Stellwagen Bank area in 1976–84, to Nantucket Shoals in 1985–87, and on Georges Bank in 1988–90 (Smith and Morse, 1993). Larval distribution data suggested that larvae from Jeffreys Ledge spawners were probably transported to Nantucket Shoals and that in subsequent years larvae from these areas were transported or adults moved to western Georges Bank and finally eastern Georges Bank (Smith and Morse, 1993). The general pattern of water circulation in the region (McGillicuddy et. al., 1988) also favors this hypothesis for the recovery.

Smith and Morse (1993) suggested that the larval survey data support the hypothesis that a recolonization of Atlantic herring occurred on Nantucket Shoals and Georges Bank. The data from their study showed a chronological pattern in larval abundance and distribution, beginning in the Gulf of Maine and progressing toward the Nantucket shoals region and finally to Georges Bank. In contrast, Stephenson and Kornfield (1990) asserted that the reappearance of herring on Georges Bank was more related to a resurgence of low numbers of stock-specific endemic fish. The autumn NMFS bottom trawl survey data tend to support the conclusions of Smith and Morse (1993) in both direction and timing. Survey indices show a progressive recovery in herring abundance from the Gulf of Maine to Nantucket Shoals, and finally to Georges Bank.

Significant changes in stock distribution, shifts in centers of primary abundance, and regional declines or disappearance of historically important spawning contingents are evident from the data. Autumn indices show that the stock component in the Gulf of Maine reached very low abundances during 1973–83 and that the Nantucket Shoals and Georges Bank components were nearly, if not actually, extirpated. Recovery times for these two components of the stock were relatively long—on the order of 10–15 years. Without a local supply of larvae, recovery was delayed considerably. Recovery was probably contingent on a supply of larval herring from the Gulf of Maine that eventually recolonized the offshore areas. Spawning restrictions along the coast of Maine and on Jeffreys Ledge in the 1980s may also have contributed to the recovery of Gulf of Maine component, thereby setting in motion the recovery of the entire stock complex.

Acknowledgments

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Recruitment of larval Atlantic menhaden (*Brevoortia tyrannus*) to North Carolina and New Jersey estuaries: evidence for larval transport northward along the east coast of the United States*

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Abstract–Age, size, abundance, and birthdate distributions were compared for larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly during their estuarine recruitment seasons in 1989–90, 1990–91, and 1992–93 in lower estuaries near Beaufort, North Carolina, and Tuckerton, New Jersey, to determine the source of these larvae. Larval recruitment in New Jersey extended for 9 months beginning in October but was discontinuous and was punctuated by periods of no catch that were associated with low water temperatures. In North Carolina, recruitment was continuous for 5–6 months beginning in November. Total yearly larval density in North Carolina was higher (15–39×) than in New Jersey for each of the 3 years. Larvae collected in North Carolina generally grew faster than larvae collected in New Jersey and were, on average, older and larger. Birthdate distributions (back-calculated from sagittal otolith ages) overlapped between sites and included many larvae that were spawned in winter. Early spawned (through October) larvae caught in the New Jersey estuary were probably spawned off New Jersey. Larvae spawned later (November–April) and collected in the same estuary were probably from south of Cape Hatteras because only there are winter water temperatures warm enough (≥16°C) to allow spawning and larval development. The percentage contribution of these late-spawned larvae from south of Cape Hatteras were an important, but variable fraction (10% in 1992–93 to 87% in 1989–90) of the total number of larvae recruited to this New Jersey estuary. Thus, this study provides evidence that some *B. tyrannus* spawned south of Cape Hatteras may reach New Jersey estuarine nurseries.

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The larvae of some species of fishes that spawn in the South Atlantic Bight (SAB; Cape Hatteras, North Carolina to Cape Canaveral, Florida) are transported northward to the Middle Atlantic Bight (MAB; Cape Cod, Massachusetts to Cape Hatteras, North Carolina) where they eventually use estuaries as juvenile nurseries. Kendall and Walford (1979) first suggested that spring-spawned bluefish, *Pomatomus saltatrix*, from the SAB are transported several hundreds of kilometers northward where they eventually enter estuaries in the MAB (Hare and Cowen, 1996). Nyman and Conover (1988) and McBride and Conover (1991) used otolith analyses to confirm the presence of a spring-spawned component from the SAB in the juvenile bluefish population in MAB estuaries. The larvae of several other species from more southerly areas are also expatriated to the MAB (Hare and Cowen, 1991; Cowen et al., 1993; McBride and Able, 1998). Tropical and subtropical planktonic invertebrates are also known to occur in the MAB (Cox and Wiebe, 1979). Some seemingly unusual occurrences of Atlantic menhaden larvae in New Jersey during the winter suggested that the same pattern might occur for this species.

Atlantic menhaden, *Brevoortia tyrannus*, is a clupeid that migrates along the coast from the Gulf of Maine to Florida and adults spawn throughout this range. Studies (summarized in Warlen, 1994; Epifanio and Garvine, 2001) have shown that this species spawns off New England from late spring into summer and again in early fall, off the mid-Atlantic states in spring and fall, and in the SAB from October to March. Maximum numbers of Atlantic menhaden probably spawn during winter in offshore waters south of Cape Hatteras (Reintjes, 1969; Judy and Lewis, 1983) and North Carolina waters are likely one of the

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major spawning grounds (Higham and Nicholson, 1964). The larvae are recruited to estuaries in North Carolina (Lewis and Mann, 1971; Warlen and Burke, 1990; Hettler and Barker, 1993; Warlen, 1994). For the purposes of this article, we define estuarine recruitment as the ingress or immigration of larvae to the estuary from the ocean.

A variety of field and laboratory observations suggest that spawning is not likely to occur at the temperatures found from late fall through spring in the MAB. Field observations in Naragansett Bay, Rhode Island (Govoni[1]), have indicated that peak densities of Atlantic menhaden eggs are found at 18–20°C and very few eggs are found at temperatures below 16°C. Kendall and Reintjes (1975) found Atlantic menhaden eggs at only one of 92 stations during one (9 November–14 December) of three late fall-winter cruises in the MAB. A summary of the Marine Monitoring Assessment and Prediction (MARMAP) collections, for November–April of the 1979–87 surveys in the MAB west of longitude 72°W from Montauk Point, New York, to Cape Hatteras, North Carolina, showed late-stage eggs in only 25 of 2247 plankton hauls (Berrien and Sibunka, 1999). Except in one haul in January near Cape Hatteras, all other Atlantic menhaden eggs found in this MAB survey were collected in November. Atlantic menhaden eggs were collected in Onslow Bay, North Carolina, in December 1992 only at temperatures of 17–23.5°C, and most were found at about 22°C (Peters[2]). During South Atlantic recruitment experiment studies (SABRE), eggs were found between the Gulf Stream and mid-shelf fronts (17–23°C) in Onslow Bay (Checkley et al., 1999). Reduced temperatures (14.8–15.7°C) appeared to diminish the ability to induce spawning of Atlantic menhaden in the laboratory (Fitzhugh and Hettler, 1995) as compared to temperatures >17°C. Even if spawning can occur at temperatures <15°C, there must be successful hatching and larval development to ensure larval survival. At 16°C, early larval growth in dry weight was about one-half that at 20°C (Powell, 1993). Therefore, we concluded that optimum temperature for hatching and larval survival and growth is probably ≥16°C.

From the above findings, we concluded that late-fall to early-spring water temperatures in the MAB are unsuitably low for Atlantic menhaden spawning. Water temperatures in the MAB to at least 300 km offshore are usually 7–14°C from mid-November through April (Benway et al., 1993a, 1993b). However, Atlantic menhaden larvae, probably spawned during that period, recruit to New Jersey estuaries from winter to spring (Witting et al., 1999). These two facts suggest a warmer water (i.e. southern) origin of the wintertime larval Atlantic menhaden recruits in New Jersey and prompted us to ask whether larval transport from the SAB could explain this occurrence. To test this hypothesis, we examined synoptic collections of larval Atlantic menhaden recruiting to estuaries in North Carolina and in New Jersey from fall to spring. We determined the duration of recruitment, age and size, relative abundance, spawning season, and relative contribution of cohorts of larvae spawned in a given calendar week to the estuarine recruitment of Atlantic menhaden larvae to an estuary in each area. These data were used to estimate the percentage of larval Atlantic menhaden collected in the New Jersey estuary that may have originated in the SAB.

[1] Govoni, J. J. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516.

[2] Peters, D. S. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC 28516.

Methods

Larval occurrence and abundance

Sampling for larval Atlantic menhaden was conducted in North Carolina and New Jersey as these larvae recruited to the estuaries from the Atlantic Ocean. In North Carolina, larvae were collected at a station adjacent to Pivers Island in the lower Newport River estuary about 2 km inside Beaufort Inlet (Fig. 1). Nighttime sampling was conducted weekly at mid-flood tide during the expected recruitment period in three seasons (15 November 1989–2 May 1990, 14 November 1990–24 April 1991, and 19 November 1992–11 May 1993). Initial seasonal sampling was based on previous years' collections (Lewis and Mann, 1971; Warlen, 1994) that showed that Atlantic menhaden larval recruitment usually began no earlier than mid-November. End-of-year sampling terminated when larval density dropped to zero. Larvae were collected in four consecutive sets of a 1×2 m neuston net with 947-µm mesh fished (most sets 5–7 minutes long) just under the surface from a bridge platform. A flow meter was attached to the net to estimate the amount of water filtered. Details of the sampling protocol are given in Warlen (1994). Ichthyoplankton samples were preserved in 95% ethanol and diluted so that the final concentration was at least 70% ethanol. Catches were standardized as the number of larvae/100 m^3 of water filtered. The mean of the density data for the four net sets on a given night was used as the density estimate of Atlantic menhaden larvae recruiting during the flood tide.

In New Jersey, gear type and sampling effort were similar in concept but differed in some details (Witting et al., 1999). Ichthyoplankton were collected with a 1-m diameter (1-mm mesh) plankton net fitted with a flow meter. The net was fished during nighttime flood tides from a bridge spanning Little Sheepshead Creek about 3 km upstream from the mouth that is approximately 2.5 km inside Little Egg Inlet (Fig. 1). Water depth at this bridge and the Pivers Island bridge was approximately 4 m. Sampling was conducted over the same years as in North Carolina, and sampling was conducted year round in New Jersey. A mean larval density (number larvae/100 m^3 water fished) was calculated from all samples on each night (five surface and five bottom sets in 1989–90, three surface and three bottom sets in 1990–91, three mid-water sets in 1992–93) and was used to estimate Atlantic menhaden larval recruitment during the flood tide. Each net set lasted 0.5 hour. Current speeds were generally 25–50 cm/s,

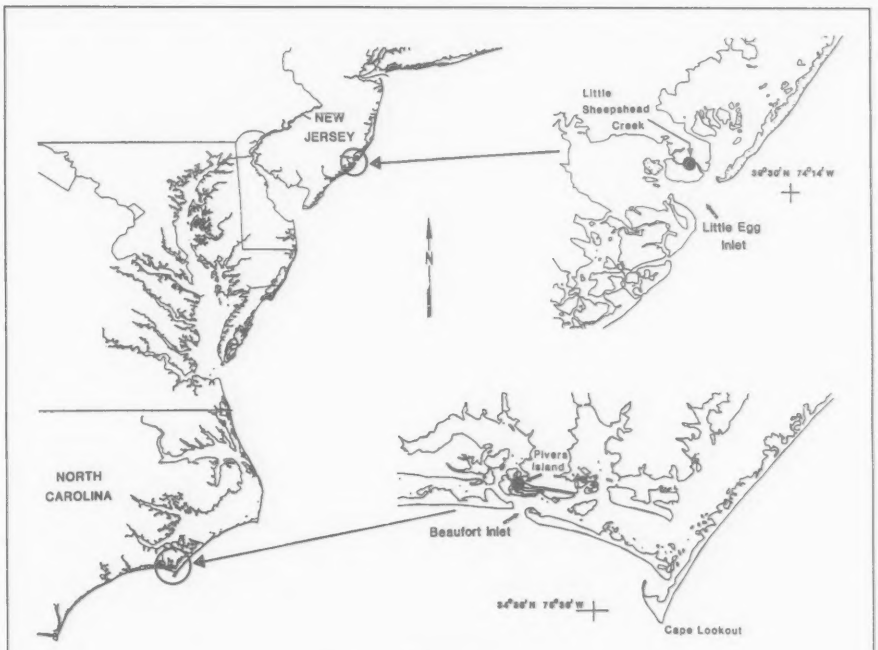

Figure 1

Location of sampling sites for larval Atlantic menhaden (*Brevoortia tyrannus*) collected at Little Sheepshead Creek, New Jersey, and Pivers Island, North Carolina, during 1989–90, 1990–91, and 1992–93.

and approximated those measured in North Carolina. As in North Carolina, samples were preserved in 95% ethanol.

We assumed that larval fish densities within and among years at a site were comparable (see Witting et al., 1999): therefore year-to-year relative abundances could be estimated at that site. However, differences between sites are not easily compared because the catch efficiency of the two types of passive nets is not known and there is no independent estimate of absolute abundance at either site.

Age, growth, and birthdate determination

Larvae were randomly subsampled from individual weekly net sets at both locations in proportion to their contribution to the total nightly catch. All larvae in catches up to 20 fish were used. In catches of >20 fish, subsample sizes were proportional to catch but generally no more than 50 fish were aged per week from any one site. Experienced otolith readers at the Beaufort Laboratory determined the ages of 1435 larvae from North Carolina and 444 from New Jersey for our study. Larvae were measured to the nearest 0.1 mm standard length (SL) with an ocular micrometer. Estimated age was the number of sagittal otolith growth increments (Maillet and Checkley, 1990) plus an empirically derived value for the number of days (five) from spawning to first increment formation (Warlen, 1992). Additionally, late-larval to early-juvenile Atlantic menhaden reared in the laboratory through the winter at ambient water temperatures, formed daily otolith growth increments even when temperatures declined to 3°C (Ahrenholz et al., 2000). We assumed that the age at initial increment deposition in larval otoliths did not vary and that otolith increment deposition rate was constant within and between sampling seasons and the two sampling sites.

To reduce the chance of underestimating ages of larvae, we conducted a detailed examination of the otolith microstructure of larvae collected in the 1990–91 season. Otoliths from fish with our assigned January–February hatching dates were re-examined and their growth increments measured on an image analysis system. One reader made all counts and measurements in close consultation with two other experienced otolith readers. In contrast to the North Carolina larvae, New Jersey larval otoliths had areas in the middle portion of the counting path with narrower increments. However, New Jersey larvae did not have checks on their otoliths, which indicated that otolith growth did not stop. The otolith radius, standard length, and age relations suggested that New Jersey fish grew more slowly than North Carolina fish but did not indicate a systematic underestimation of the age of New Jersey fish due to narrow increments.

Average growth of larvae was described by the Laird version (Laird et al., 1965) of the Gompertz growth equation (Zweifel and Lasker, 1976). The model was fitted to

data for SL and estimated age at time of capture. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation (Warlen, 1992). Because the conventional 3-parameter fit produced two cases where the estimates of the model intercept ($L_{(0)}$) were biologically unreasonable, all data sets were rerun by using a 2-parameter (i.e. $A_{(0)}$ and α) fitting procedure and by setting the intercept (third parameter) at 3.5 mm. This size at hatching was an intermediate value between the estimates of Powell and Phonlor (1986) for Atlantic menhaden hatching at 16° and 24°C. The overall average growth rate from hatching to a given age was the quotient of the predicted size at that age minus the size at hatching (3.5 mm) divided by that age. Differences in population growth curves between sampling locations in each year were tested by using a 2-parameter Hotelling's T^2 test of the model parameters (Bernard [1981] as modified by Hoenig and Hanumara[3]).

The birthdate (=spawning date) of each larva was back-calculated by subtracting its estimated age from the date of capture. Birthweek cohorts were defined as larvae spawned in a given calendar week. Density values and percentage age composition of each week's catch were used to estimate the estuarine recruitment of birthweek cohorts for each year and each location by using the methods of Warlen (1994). Birthdate distributions were used to estimate the percentage of larval recruits to the New Jersey estuary that could have originated in the SAB. The menhaden spawning season in North Carolina and New Jersey was estimated from the birthdate distributions of larvae that survived to enter the estuaries. The percentage distribution of spawning by week was based on the relative abundance of larvae collected throughout each recruitment year.

We assumed that larval Atlantic menhaden caught each week were newly recruited to the estuary and that they were in transit past the sampling sites to upper portions of the estuaries. This assumption is supported by the arguments in Warlen (1994), Churchill et al. (1999), and Forward et al. (1999) for the North Carolina sampling site and the patterns observed for other shelf-spawned estuarine dependent species such as summer flounder (*Paralichthys dentatus*) (Keefe and Able, 1993; Able and Kaiser, 1994) and other species for New Jersey (Witting et al., 1999).

Results

Timing and abundance of larval recruitment

The magnitude of larval Atlantic menhaden recruitment appeared to differ substantially between the two locations (Fig. 2). The sum of the weekly mean larval densities

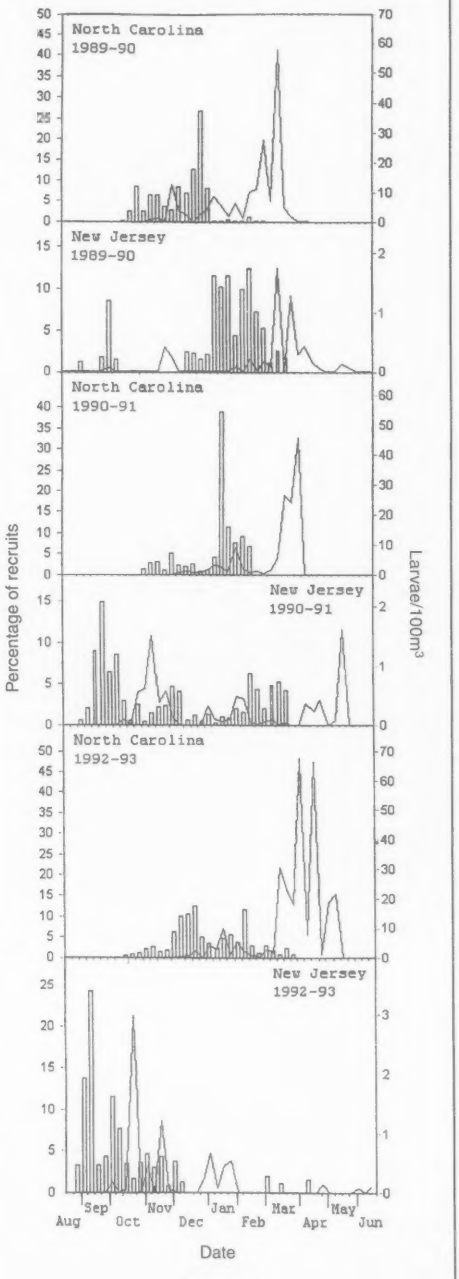

Figure 2

Weekly mean density (larvae/100 m^3) (line graph) and birthdate frequency distributions (bar graph) as calculated from relative abundances of larval Atlantic menhaden (*Brevoortia tyrannus*) in collections at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during 1989–90, 1990–91, and 1992–93.

[3] Hoenig, N. A., and R. G. Hanumara. 1983. Statistical considerations in fitting seasonal growth models for fishes, 25 p. ICES council meeting 1983/D.

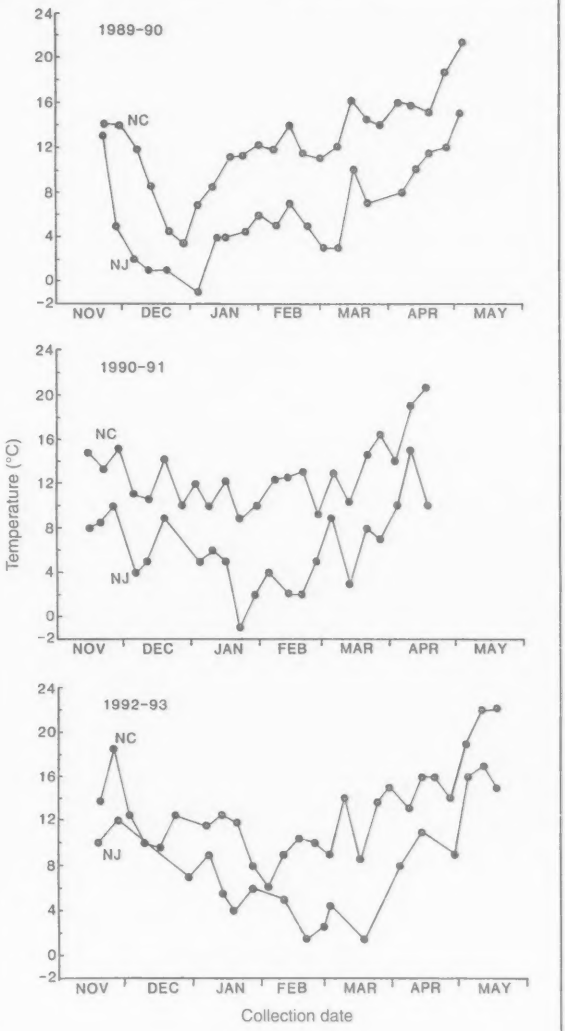

Figure 3

Surface water temperature at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during collections in 1989–90, 1990–91, and 1992–93.

over all collections was a measure of the total abundance during a year. The total yearly densities (larvae/100 m^3) for North Carolina were 173 (1989–90), 128 (1990–91), and 286 (1992–93) and for New Jersey were 5.5 (1989–90), 8.4 (1990–91), and 7.3 (1992–93). Although there appeared to be generally large differences in overall abundance between the two areas, we could not determine how much of the 15–39× difference was due to the geographic location, the catch efficiency of the two types of gear, or to differences in sampling effort. Nightly mean densities were always low in New Jersey and, with one exception (20 October 1992), never exceeded 2.0 larvae/100 m^3, whereas in North Carolina nightly catches could exceed 40 larvae/100 m^3 every season (Fig. 2).

There were apparent differences in the timing of larval Atlantic menhaden entering estuaries in North Carolina and New Jersey (Fig. 2). Larval recruitment in New Jersey, which extended over a longer period (8–9 months) than that in North Carolina (5–6 months), began in October and ended in June (Fig. 2). Recruitment in New Jersey was discontinuous and was punctuated by periods of no catch, usually in late fall to early spring. The absences of

larval catches in some periods in New Jersey are associated with low water temperatures. There were no larvae caught in December–January of 1989–90 and 1990–91 and in February–March 1993 when water temperatures remained between 1.0 and 5.0°C (Fig. 3). In contrast, recruitment in North Carolina began in November and was continuous until ending in April or May (Fig. 2). Water temperature in North Carolina was warmer than in New Jersey and only twice dropped below 6°C (Fig. 3). In all three years in North Carolina, recruitment was characterized by a late season peak that occurred in March or April (Fig. 2). Predominant recruitment in New Jersey occurred either early (1992–93), late (1989–90) or with peaks early and late in the season (1990–91).

Larval age and size

Menhaden larvae entered both estuaries after development in the ocean. Most larvae were >1 month old and ≥ 17 mm long and there were no recently hatched specimens. However, the age and size of larvae entering the two estuaries differed within and between sites. The weekly mean age of Atlantic menhaden larvae collected in North Carolina increased linearly from early in the season to about the end of March in each year (Fig. 4). The weekly mean age over this period increased by a factor of 2–3×. In two years (1990, 1993) the mean age declined after March to levels approximating those early in the recruitment season. Larvae collected in the North Carolina estuary during peak recruitment were also the older (and larger) larvae. In New Jersey, although there was a general increase in larval age between October and December, there was no late season decline in mean age as we observed for North Carolina larvae. Larvae collected in New Jersey were generally younger than those collected in North Carolina for each of the three years (Fig. 5). The overall mean age of larvae collected in North Carolina for 1989–90, 1990–91, and 1992–93 were 60.7, 58.6, and 69.3 d as compared to 54.3, 52.7, and 50.9 d for New Jersey, respectively. The size of larvae showed seasonal trends similar to those for larval ages in each of the years, i.e. larval length increased and then decreased through time in North Carolina, whereas in New Jersey it increased but did not decline (Fig. 6). Larvae recruited in North Carolina were generally similar in size but were on average larger (24.9, 25.4, and 25.8 mm) than larvae recruited in New Jersey (22.2, 21.3, and 22.1 mm) in all three years (Figs. 6 and 7).

Growth of larvae

Larvae collected in North Carolina were generally older and larger and grew faster than larvae in New Jersey (Fig. 8). Population growth curves were significantly different between sampling locations in all years (Table 1). The predicted overall average growth rate from hatching to 65 d for larvae recruited in North Carolina was similar among years (0.35 mm/d for 1989–90, 0.36 mm/d for 1990–91, and 0.35 mm/d for 1992–93). Corresponding rates for larvae recruited to New Jersey were 0.30 mm/d for 1989–90, 0.31mm/d for 1990–91, and 0.32 mm/d for 1992–93.

Larval birthdates

Back-calculated spawning dates varied between years in both locations but were most variable in New Jersey (Fig. 2). In New Jersey in the 1989–90 season there were two distinct groups of larvae. About 13% of the larvae were spawned early (September–October), then none to the middle of December, and the remaining larvae (87%) were spawned thereafter to the end of March. Larvae captured in North Carolina were spawned from the week ending 21 October 1989 continuously through the week ending 3 March 1990 and overlapped the later spawning dates for New Jersey larvae. Larvae spawned in March recruited to New Jersey but virtually none recruited to North Carolina.

In the 1990–91 season, spawning dates of larvae collected in New Jersey (7 months) totally overlapped those collected in North Carolina (4 months) (Fig. 2). About 45% of the New Jersey larvae were spawned early (through week ending 27 October 1990) and the balance was distributed over the last five months with a mode in the week ending 23 February 1991. As in 1989–90, March-spawned larvae recruited to New Jersey but not to North Carolina. The highest frequency of spawning dates of larvae caught in North Carolina occurred from mid-January to the end of the season and peaked during the week ending 26 January 1991.

The spawning date distributions in 1992–93 were different from those in the previous two sampling seasons. About 77% of the New Jersey larvae were spawned by the end of October. An additional 18% of the total larvae entering the estuary were spawned in November to mid-December and only about 5% of the total were spawned in March–April. Larvae recruited to North Carolina had been spawned from October to April but there was no distinct mode as observed in the other two years. Late season spawning (March–April) contributed larvae to both New Jersey (≈5% of total) and North Carolina (≈13% of total). In both earlier years there were no April-spawned larvae and March-spawned larvae were only found in New Jersey.

Discussion

Atlantic menhaden larvae recruited to the New Jersey estuary probably originate from two sources: locally (MAB) and from the SAB. Evidence of local spawning is seen in the larvae recruited to the New Jersey estuary from October through early December (Fig. 2). These larvae probably originated from local (i.e. New Jersey) spawning as adults begin their southward migration out of the MAB area in about November of each year (Higham and Nicholson, 1964). Schools of spawning-size adults (200 mm+) are captured in the commercial fishery in the fall and early winter as they move south along the coast from Maryland to North Carolina (Smith[4]). Spawning in the SAB produces larvae, some of which are transported northward and contribute recruits to New Jersey later in

[4] Smith, J. W. 1996. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC.

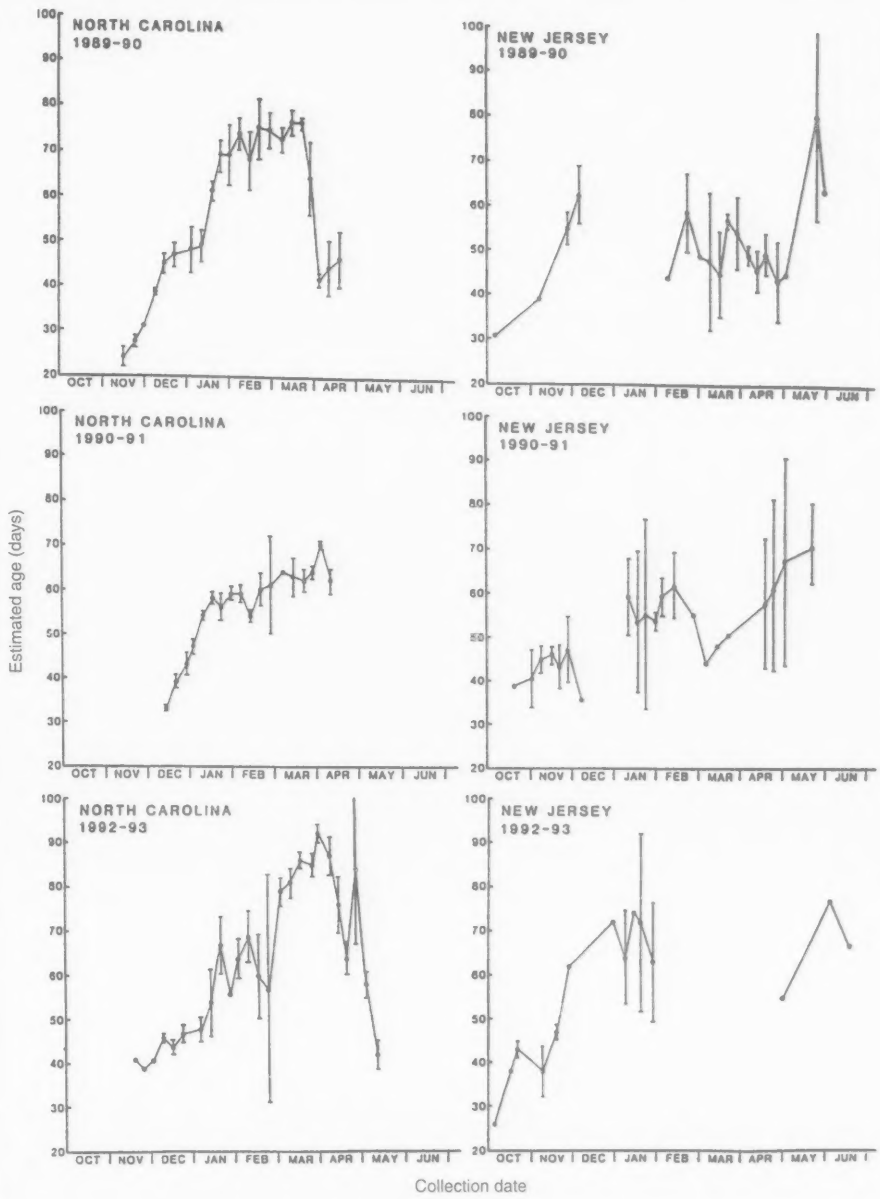

Figure 4

Mean of estimated age (days) with 95% confidence limits of larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during their estuarine recruitment in 1989–90, 1990–91, and 1992–93.

the recruitment season. Some larvae originating in the southernmost portion of the MAB in fall may even contribute some recruits to the SAB as three-dimensional circulation models have predicted (Quinlan et al., 1999; Rice et al., 1999; Stegmann et al., 1999). However, any adults that might remain in the MAB after November would experience ocean temperatures on the continental shelf that are not only too cold to allow menhaden spawning but that also might prevent eggs from hatching or larvae from developing. Even if we accept the minimum temperature of 13°C

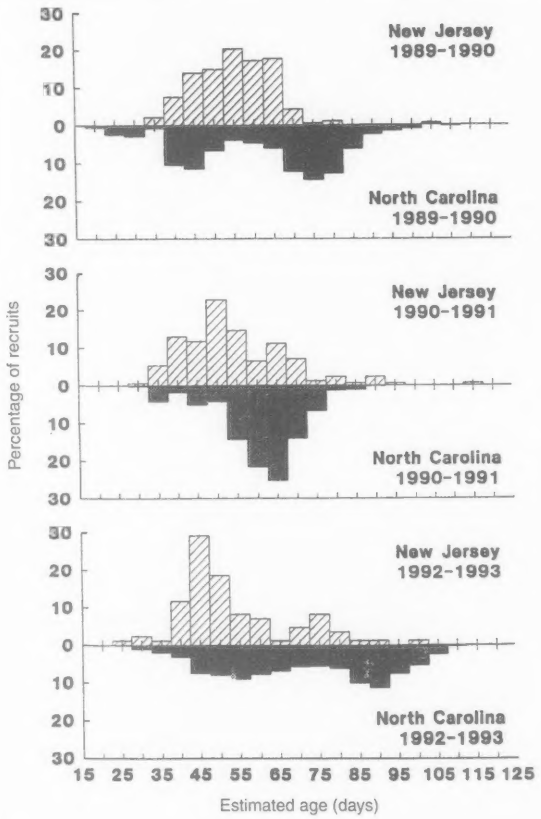

Figure 5

Percentage distribution of estimated age (5-d intervals) for larval Atlantic menhaden (*Brevoortia tyrannus*) recruited to Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–91, and 1992–93.

for Atlantic menhaden spawning suggested by Stegmann et al. (1999), there were no water temperatures above 12°C in the MAB in December through March (Fig. 9) during the three years of our study.

Two differing hypotheses could explain the occurrence of menhaden larvae recruiting to the New Jersey estuary in winter and spring. One is that larvae spawned in the MAB in October or November remain in the MAB until they move into estuaries in the spring. This hypothesis would require a retention mechanism to keep larvae on the continental shelf over the winter in water <10°C. No such mechanism is likely as field and modeling studies indicate persistent southwestward transport (Pietrafesa et al., 1994; Churchill and Berger, 1998; Werner et al., 1999). If larvae overwintered on the continental shelf, they would be about 150–210 d old when they recruited to the estuary 5–7 months after spawning. No Atlantic menhaden this old were found in any of the samples, or from any other studies (Warlen, 1994; Rice et al., 1999), and underaging of larval otoliths in our study did not appear to be a problem.

An alternative but more feasible hypothesis for the observed winter-spawned larvae collected in New Jersey from December to the end of the recruitment season (May–June) is that they were spawned in the SAB and were transported northward to the MAB. We used the density-weighted, back-calculated spawning date distributions of larvae collected in New Jersey that were spawned from November to April as the best estimator of the percentage of the total recruits that were spawned in the SAB. If we use the portion of larvae spawned December or later as the most conservative estimator, then the contribution of larvae from the SAB, of all New Jersey recruits, was 87% in 1989–90, 47% in 1990–91, and 10% in 1992–93. If larvae spawned November or later are considered to be from the SAB where there was spawning, then the estimate (87%) is the same for 1989–90 but increases to 55% in 1990–91 and to 23% in 1992–93.

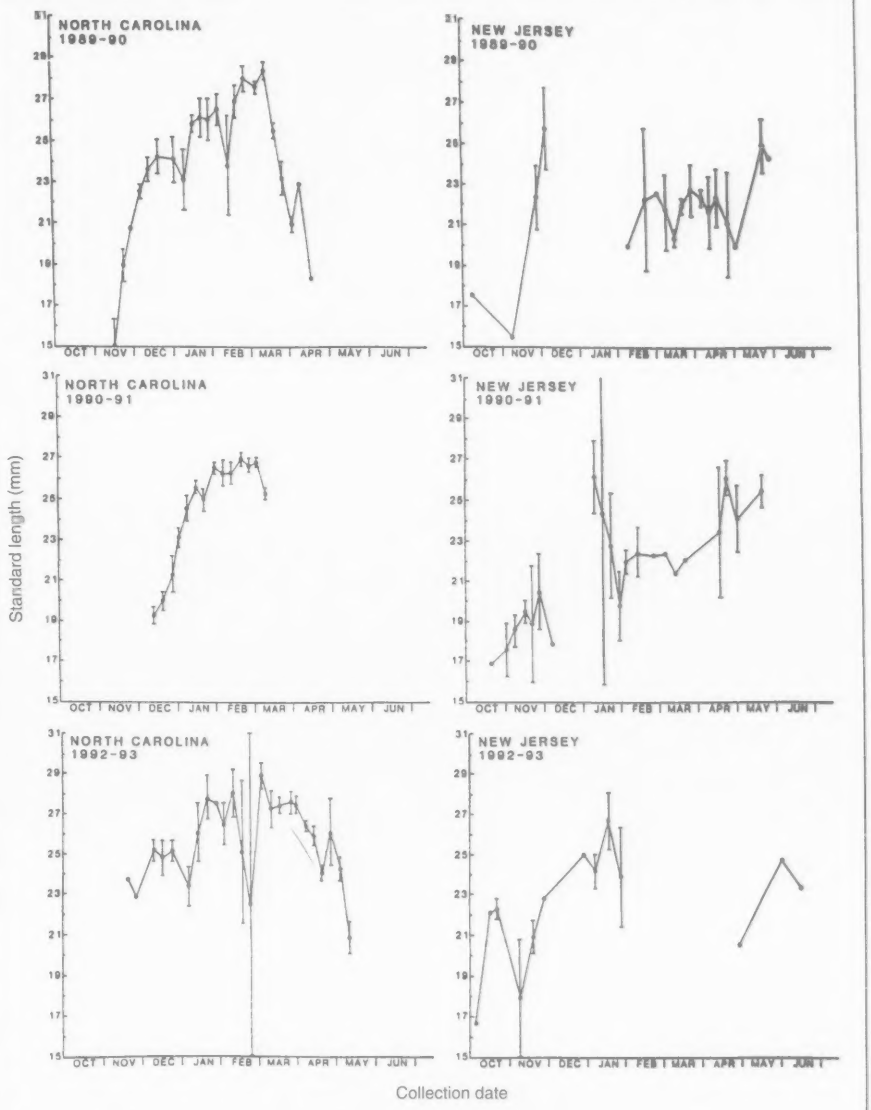

Figure 6

Mean standard length (mm) with 95% confidence limits of larval Atlantic menhaden (*Brevoortia tyrannus*) collected weekly at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, during their estuarine recruitment in 1989–90, 1990–91, and 1992–93.

Although the estimated percentage of larvae contributed to the New Jersey estuary from the SAB varied between 10% and 87%, the actual numbers of contributed larvae were relatively low, over an order of magnitude less than that observed for North Carolina, because of the overall low number of larvae recruited there. However, the total contribution of SAB larvae to New Jersey recruitment over the entire season may actually be greater than estimated from the birthdate distributions. The contribution of larvae spawned in the MAB to recruitment in New Jersey is based on the presence of early season larvae, but for these fish to contribute to the population the next spring, they must survive the winter in the estuary. If the winter water temperature in New Jersey estuaries drops below the lethal limit for Atlantic menhaden larvae (<5.0°C; Lewis, 1965), there will be decreased survival for the fall

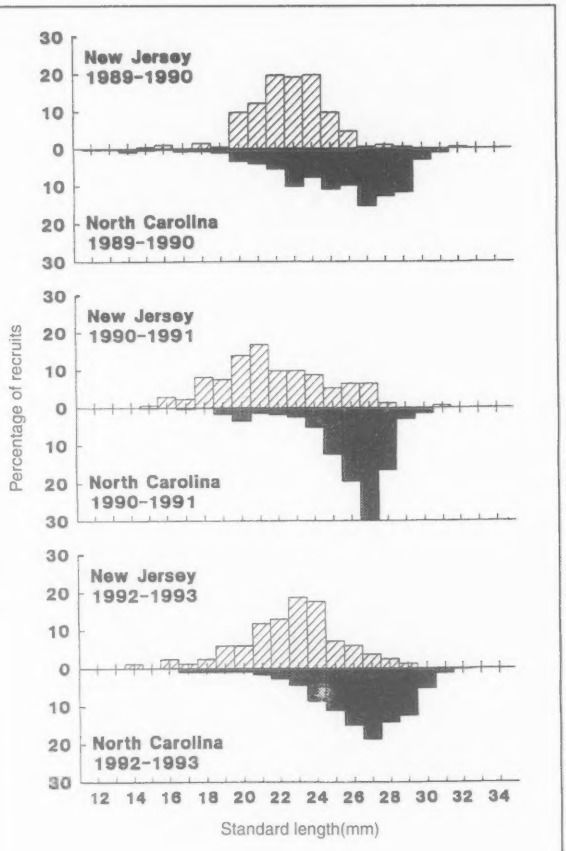

Figure 7

Percentage distribution of standard length (1-mm length intervals) for larval Atlantic menhaden (*Brevoortia tyrannus*) collected during their recruitment at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–91, and 1992–93.

recruited larvae. Temperatures this low are often found during winter in New Jersey estuaries (Able et al., 1992) and result in mortality of several other estuarine species (Szedlmayer et al., 1992; Keefe and Able, 1993; Hales and Able, 2001). We did not catch Atlantic menhaden larvae in the New Jersey estuary at any time when the surface water temperature was <5°C. Temperatures <3°C deterred larval Atlantic menhaden entry into estuaries, inhibited movements into tributaries, and caused mass mortalities in Indian River, Delaware (Reintjes and Pacheco, 1966). Alternatively, larvae recruiting in March or later have less chance of encountering lethal temperatures and experiencing cold-related mortality and hence their proportion of the total year's recruitment may increase.

The precise mechanisms responsible for larval Atlantic menhaden transport from the SAB to the MAB are unknown. However, it seems likely that larvae may be transported northward by the Gulf Stream. Atlantic menhaden larvae that are spawned on the outer continental shelf of North Carolina (Checkley et al., 1988; Warlen, 1992; Govoni and Pietrafesa, 1994) may be entrained in meanders that impinge onto the shelf (Pietrafesa et al., 1985) and carried northward out of the SAB. Govoni and Spach (1999) estimated offshore fluxes of Atlantic menhaden larvae from the North Carolina shelf to the Gulf Stream during the winter. Modeling results supported these empirical findings and indicated that export from the North Carolina shelf is influenced by both wind and bathymetry (Hare et al., 1999). Once in the Gulf Stream, larvae can be transported rapidly (≈100 cm/s) to the northeast (Hare[5]).

[5] Hare, J. A. 1999. Personal commun. Center for Coastal Fisheries and Habitat Research, National Ocean Service, NOAA, 101 Pivers Island Rd., Beaufort, NC.

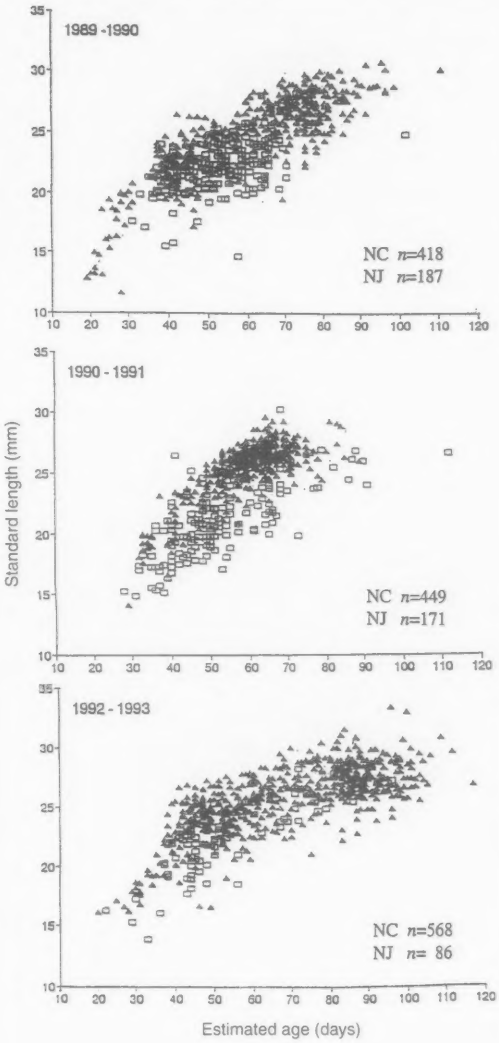

Figure 8

Summary plots of standard length (mm) on estimated age (days) for larval Atlantic menhaden (*Brevoortia tyrannus*) collected at Pivers Island, North Carolina, and Little Sheepshead Creek, New Jersey, in 1989–90, 1990–9, and 1992–93.

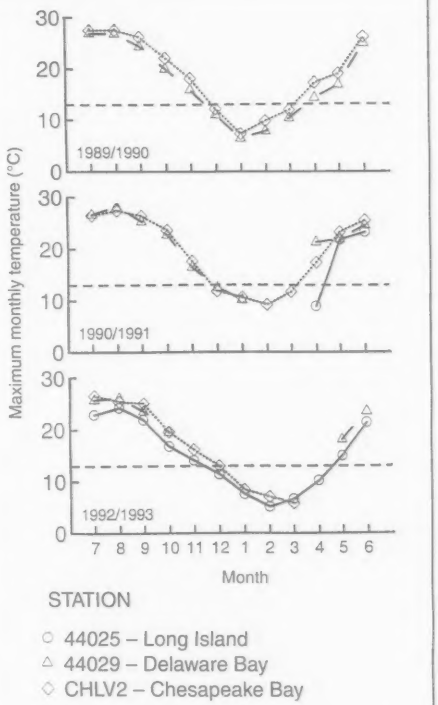

Figure 9

Maximum monthly sea surface temperatures recorded at three NOAA stations in the Middle Atlantic Bight that encompassed the time periods of our three sampling years. Minimum temperature that *Brevoortia tyrannus* eggs had been caught during MARMAP surveys (13°C; Stegmann et al., 1999) are indicated by a horizontal dashed line. In months with maximum temperatures below 13°C no spawning of *B. tyrannus* north of Cape Hatteras was expected. NOAA Data Buoy 44025 located ~45 km south of Long Island, New York at 40°15′1″N, 73°10′0″W. NOAA Data Buoy 44029 is located ~45 km southeast of Delaware Bay at 38°27′49″N, 74°42′7″W. NOAA C-MAN station CHLV2 is located ~20km east of Chesapeake Bay at 36°54′18″N, 75°42′48″W.

Warm core ring streamers and surface intrusions of warmer water could assist in transporting larvae from the Gulf Stream to the MAB continental slope (Hare and Cowen, 1991, 1996). Larvae must then cross the shelf-slope front and once larvae are in shelf waters they may be transported south and westward along the coast and toward shore by the predominant winds from the northeast which induce an Eckman drift westward toward shore. Biological mechanisms such as vertical migrations and directional swimming behavior, can modulate transport by placing larvae in water masses favorable to cross slope or cross shelf transport (Hare and Cowan, 1996). Cowen et al. (1993) and Hare and Cowen (1993) have described this general scenario for several species that may be transported to the MAB from the SAB.

Regardless of the type of transport mechanisms, it is clear that larvae of a number of other species are transported from the SAB to the MAB. The larvae of *Anguilla rostrata*, which originate in the Sargasso Sea (Schmidt,

Table 1

Estimates of Gompertz growth model parameters ($A_{(0)}$, α) with standard errors in parentheses for larval Atlantic menhaden collected in 1989–90, 1990–91, and 1992–93 in North Carolina and New Jersey and results of Hotelling's T^2 tests comparing growth models between sites for each year. In each model fit, $L_{(0)}$ was set at 3.5 mm standard length. * Significant at 0.01.

	Year		
Statistics	1989–90	1990–91	1992–93
Growth model[1]			
North Carolina			
$A_{(0)}$	0.113 (0.002)	0.101 (0.001)	0.113 (0.002)
α	0.054 (0.001)	0.048 (0.001)	0.055 (0.001)
New Jersey			
$A_{(0)}$	0.129 (0.008)	0.092 (0.003)	0.104 (0.005)
α	0.068 (0.005)	0.046 (0.002)	0.051 (0.003)
Hotelling's T^2			
Sample size			
n_1—NC	418	449	568
n_2—NJ	187	171	85
$F(0.01 f_1 f_2)$[2]	5.30	5.30	5.30
$F_{(calculated)}$	153.87*	127.81*	7.12*

[1] $L_{(0)}$ = length at hatching, $A_{(0)}$ = specific growth rate at hatching, α = exponential decline in $A_{(0)}$.
[2] 0.01 = level of testing, f_1 = np (=no. of parameters), $f_2 = n_1+n_2-np-1$.

1922; McCleave and Miller, 1994), occur in and near the Gulf Stream in the SAB and appear as glass eels in the New Jersey collections at approximately the same time as menhaden larvae (Witting et al., 1999). The same general track is presumed for *Conger oceanicus* which also spawn in the Sargasso Sea (Miller, 1995) and are also collected at the New Jersey study site, although they occur later (May–June) (Able and Fahay, 1998; Witting et al., 1999). Similarly, other species which presumably spawn in the SAB such as *Chaetodon* spp. (McBride and Able, 1998), *Mugil curema* (Collins and Stender, 1989), and *Lutjanus griseus* (Able and Fahay, 1998) also enter the New Jersey study site (Able et al., 1997; Witting et al., 1999). Larval spot, *Leiostomus xanthurus,* spawned south of Cape Hatteras may also be transported to estuaries in the MAB (Norcross and Bodolus, 1991).

In summary, although the SAB may be a very important spawning area for Atlantic menhaden, all larvae produced in the SAB are not retained there; some are transported to the MAB. We believe the birthdate distribution data suggest that Atlantic menhaden larvae spawned in the SAB are an important but variable source of recruits (10–87%) for the MAB based on the collections from New Jersey. The number of winter-spawned larvae ultimately recruited to New Jersey probably depends on the initial number of larvae transported northward from the SAB, the efficacy of the transport mechanisms, and the mortality of larvae during the process. Obviously, the estimates for this single New Jersey estuary may differ from other areas in the MAB. As a result of the above variables and recent insights from the SABRE program, it appears that larval Atlantic menhaden supply is very complex with frequent exchanges between the MAB and the SAB, as well as the contribution from local spawning. Ultimately, we need to know which spawning seasons and sites contribute most individuals to nursery habitats (Beck et al., 2001) and to the adult population.

The relative contribution of SAB menhaden larvae, and those of other species, to other estuaries in the MAB might clarify the importance of MAB estuaries and contribute to an improved understanding of recruitment mechanisms for shelf-spawned estuarine-dependent fishes in the MAB. Additional evidence for the contribution of SAB larvae to the MAB could come from analyses of the elemental composition of the primordium (nucleus) of larval otoliths from both New Jersey and North Carolina. The laser ablation inductively coupled plasma mass spectroscopy (ICPMS) technique (Campana et al., 1994; Thorrold et al., 2001) might be used to discriminate among larvae to determine if they have similar or different geographic origins. Similarities in elemental composition of New Jersey and North Carolina larvae with the same winter-spawned birthdate would be an important step toward validating the common geographic origin of the larvae recruited to New Jersey and perhaps elsewhere in the MAB.

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Origin of immature loggerhead sea turtles (*Caretta caretta*) at Hutchinson Island, Florida: evidence from mtDNA markers

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Abstract–Loggerhead sea turtles (*Caretta caretta*) are migratory, long-lived, and slow maturing. They are difficult to study because they are seen rarely and their habitats range over vast stretches of the ocean. Movements of immature turtles between pelagic and coastal developmental habitats are particularly difficult to investigate because of inadequate tagging technologies and the difficulty in capturing significant numbers of turtles at sea. However, genetic markers found in mitochondrial DNA (mtDNA) provide a basis for predicting the origin of juvenile turtles in developmental habitats. Mixed stock analysis was used to determine which nesting populations were contributing individuals to a foraging aggregation of immature loggerhead turtles (mean 63.3 cm straight carapace length [SCL]) captured in coastal waters off Hutchinson Island, Florida. The results indicated that at least three different western Atlantic loggerhead sea turtle subpopulations contribute to this group: south Florida (69%), Mexico (20%), and northeast Florida-North Carolina (10%). The conservation and management of these immature sea turtles is complicated by their multinational genetic demographics.

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North Atlantic loggerhead sea turtles have extended and complex developmental life histories (Musick and Limpus, 1997). After emerging from their nests, hatchling loggerhead sea turtles enter the surf and eventually move into the pelagic environment for several years before returning to inshore benthic coastal waters. The accepted hypothesis is that these hatchlings are passively transported to the eastern Atlantic by major current systems and these turtles would eventually return to coastal benthic habitats in the western Atlantic by the North Atlantic gyre when they attain 25–60 cm or an estimated 3–10 years old (Carr, 1986, 1987; Musick and Limpus, 1997).

The loggerhead sea turtle (*Caretta caretta*) is listed as threatened under the United States Endangered Species Act of 1973 and subsequent amendments. Although the loggerhead sea turtle nesting population in the southeastern United States is one of the largest in the world, other distinct nesting populations (as defined by genetic divergence) exist in the northwestern Atlantic Ocean. These known subpopulations are found in the Yucatan, northwest Florida, south Florida, and from north Florida to North Carolina. The east central coast of Florida supports the largest nesting subpopulation of loggerhead turtles and is a highly dynamic coastal area with multiple sea turtle species in various postpelagic developmental stages (Witzell, 1987). Sea turtles may hatch in one country, grow through adolescence in a second or more countries, feed and reproduce as adults in a third jurisdiction, and swim through a dozen more territorial waters enroute to and from these destinations (Bowen et al., 1995). Tagging studies, unfortunately, are only capable of providing glimpses of these complex changes in developmental habitats because of high tag loss rates and rare opportunities of recapturing tagged turtles thousands of kilometers away in the pelagic environment several years later (Chaloupka and Musick, 1997).

The likelihood that turtles from genetically distinct stocks share coastal and pelagic developmental habitats may raise doubts regarding the effectiveness of conservation strategies based on geographical or political boundaries (Carr and Stancyk, 1975; Bowen and Witzell, 1996). Consequently, sea turtle biolo-

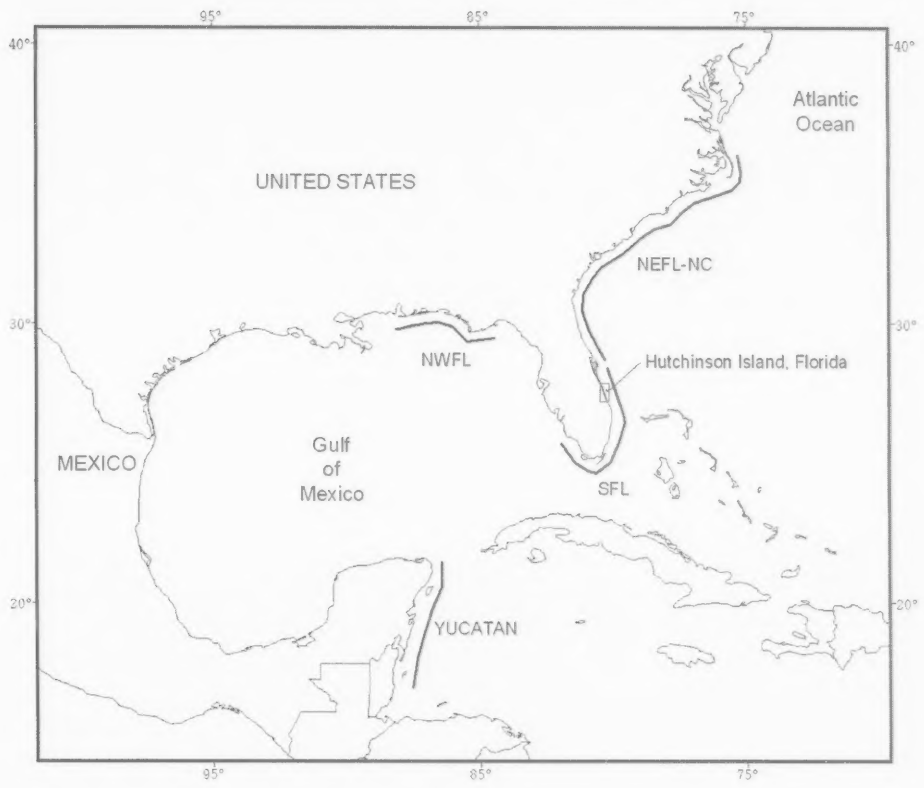

Figure 1

Locations for which are known loggerhead sea turtle nesting haplotypes and the location of the Hutchinson Island foraging population.

gists and marine resource managers are presented with complex challenges that reinforce the need for complete life history information. In particular, the origin of immature loggerhead sea turtles foraging in coastal nearshore waters needs to be determined for the development of effective regional conservation and management strategies. Recent research has demonstrated that most sea turtle nesting colonies are genetically distinct as indicated by mitochondrial (mt) DNA haplotype frequency shifts. This finding allows the possibility of using mtDNA data to identify rookery cohorts on feeding grounds (Bass et al., 1998; Broderick et al., 1994). By using an existing database (Encalada et al., 1998) and molecular techniques, tissue samples from juvenile marine turtles can be analyzed to estimate the origin of animals inhabiting developmental habitats. These data are collected and analyzed faster than results from tagging studies and may provide information on cryptic migratory behavior (Bowen et al., 1995; Bolten et al., 1998). Both pelagic and coastal benthic zones are believed to be essential developmental habitats for sea turtles, and molecular markers have recently been used to document shifts in the demographic composition between these habitats (Laurent et al., 1998). This article examines the mtDNA composition of juvenile loggerhead sea turtles using the coastal waters off Hutchinson Island, Florida, to determine whether the turtles are primarily from the adjacent nesting subpopulation or whether this foraging population is composed of individuals from multiple rookeries.

Materials and methods

Sea turtles are routinely captured in the canal that supplies cooling water at the St. Lucie Power Plant on Hutchinson Island, Florida (Fig. 1). The power plant intake operates year round—collecting sea turtles from 365 m offshore and providing an excellent opportunity to sample sea turtles in the nearshore developmental habitat (Bass and Witzell, 2000). Power plant biologists collect these turtles daily in an ongoing research and conservation program. Turtles are measured, flipper-tagged, and released in good condition promptly into the adjacent coastal waters.

A total of 109 juvenile loggerhead sea turtles were sampled at the St. Lucie power plant from January through May 1999 for our study. The minimum straight carapace length (SCL) was measured with calipers. Tissue samples were collected by using a 6-mm biopsy punch and placed in 15 mL of saturated salt preservation buffer developed

Table 1

Haplotype distribution among loggerhead sea turtle nesting groups compiled by Encalada et al. (1998). Haplotypes K and M were identified previously in the Madeira and Azores foraging assemblages (Bolten et al., 1998). Haplotype N was identified previously in a sample of stranded individuals from the Atlantic U.S. coast (Rankin-Baransky et al., 2001).

Haplotype	NWFL	SFL	NEFL-NC	Mexico	Greece	Brazil	St. Lucie, Florida
A	34	22	104	—	—	—	40
B	4	24	1	11	19	—	45
C	2	2	—	2	—	—	7
D	—	—	—	—	—	11	11
E	—	1	—	—	—	—	—
F	—	—	—	—	—	—	—
G	2	1	—	—	—	—	—
H	—	—	—	1	—	—	—
I	—	—	—	1	—	—	4
J	—	—	—	5	—	—	2
K	—	—	—	—	—	—	1
M	—	—	—	—	—	—	1
N	—	—	—	—	—	—	1

by Amos and Hoelzel (1991). Samples were transferred to the University of Florida for analysis. Standard phenol and chloroform DNA isolation protocols were conducted on the tissue samples (Hillis et al., 1996). A 380-bp fragment of the mitochondrial DNA control region was amplified using primers

TCR5 (5′-TTGTACATCTACTTAATTACCAC-3′), and

HDCM2 (5-GCAAGTAAAACTACCGTATGCCAGGTTA-3′)

designed for sea turtles (Encalada et al., 1996; Norman et al., 1994). Cycling parameters were as follows: 94°C 1 min, 25 cycles of (94°C/45s + 52°C/30s + 72°C/45s) and 3-min extension at 72°C.

Individuals were compared to known loggerhead sea turtle haplotypes and assigned a letter designation based on Encalada et al. (1998) and Bolten et al. (1998). To test for statistical differences among haplotype frequencies at rookeries and the foraging location, chi-square analyses were performed with the program CHIRXC (Zaykin and Pudovkin, 1993) and probabilities were generated with a Monte Carlo randomization procedure (Roff and Bentzen, 1989).

Maximum likelihood (ML) analysis for mixed stock identification (Grant et al., 1980) was used to estimate the contributions of nesting populations to the foraging habitat adjacent to the St. Lucie Power Plant on Hutchinson Island. This method estimates the most likely contributions of source populations based on the haplotype frequencies in the source populations and in the mixed population. The source populations and frequencies of associated haplotypes used in the analysis were those of Encalada et al. (1998). It should be noted that the addition of new nesting population data could change the results presented in our study. The addition of new nesting data will always be a problem when conducting these types of analyses but should not preclude the use of this technique to determine potential contributors to a foraging population. The maximum likelihood program GIRLSEM was used (Masuda et al., 1991). As a starting point in ML iterations with GIRLSEM, it was assumed that all source populations had an equal probability of contributing (i.e. population size, distance from the foraging location, etc. did not have an impact on the percentage of animals recruiting to a particular area). Standard errors and 95% confidence intervals of the point estimates were generated from 100 bootstraps of the stock and mixture data sets with GIRLSEM (Pella et al., 1998).

Results

Mitochondrial DNA analysis

Of the 109 tissue samples collected, 106 produced readable sequences (Table 1). Eighty five of the samples consisted of the most common haplotypes A and B. Haplotype C, another haplotype found in multiple rookeries at low frequency, was found in seven individuals. One individual was characterized by haplotype G, known only in the northwest Florida (NWFL) and south Florida (SFL) source populations. Two haplotypes "endemic" to Mexico (Yucatan), I and J, were found in six of the individuals sampled. The remaining seven individuals possessed haplotypes (K, M, and N) observed previously, but only from surveys of foraging or stranded individuals.

The haplotype frequencies of the foraging juveniles were significantly different from all nesting loggerhead sea turtle populations except for the SFL nesting population (χ^2=9.51, P=0.40). Although the haplotype frequencies were similar to that of the SFL nesting population, the presence of haplotypes not associated with the SFL popu-

Table 2

Maximum likelihood estimates of contribution by source populations to immature loggerhead sea turtles from the St. Lucie Power Plant (n=99). Estimates were generated by using UCON software (Masuda et al., 1991) Standard errors and 95% confidence intervals were generated from 100 bootstraps of both the stock and mixture using GIRLSEM. NWFL = northwest Florida; SFL = south Florida; and NEFL-NC = northeast Florida to North Carolina.

Source population	Contribution	Standard error	95% Confidence interval
NWFL	0.0912	0.1896	0.0479–0.1345
SFL	0.6681	0.3072	0.5979–0.7383
NEFL-NC	0.0366	0.1363	0.0055–0.0677
Yucatan	0.2040	0.1125	0.1783–0.2297
Brazil	0.0000	0.0000	—
Greece	0.0000	0.1555	0.0000–0.0355

Table 3

Maximum likelihood estimates of contribution by source populations to immature loggerhead turtles from the St. Lucie power plant (n=99). Estimates were generated by using UCON software (Masuda et al., 1991). Standard errors and 95% confidence intervals were generated from 100 bootstraps of both the stock and mixture by using GIRLSEM. The source populations NWFL, Brazil and Greece, were removed from the analysis. SFL = south Flordia; and NEFL-NC = northeast Florida to North Carolina.

Source population	Contribution	Standard error	95% Confidence interval
SFL	0.6965	0.2211	0.6527–0.7403
NEFL-NC	0.0984	0.1151	0.0756–0.1212
Yucatan	0.2050	0.1296	0.1793–0.2307

lation indicates that this nesting population is not the sole contributor to this foraging population.

Maximum likelihood analysis

The initial maximum likelihood analysis yielded estimates of contribution that were associated with high standard errors (Table 2). The estimate for NWFL had an extremely high standard error. This high standard error is an indication of sampling error associated with the source population (Epifanio et al., 1995). Because of the large standard errors, an attempt was made to reduce the complexity of solutions that were involved in the maximum likelihood algorithm's search. Removing a potential source population decreases the potential number of "answers," consequently reducing the standard errors about the mean estimates.

The maximum likelihood analysis was repeated, removing the smallest and most distant source populations (NWFL, Brazil, and Greece) as potential contributors (Table 3). In addition to the statistical assumption that the large variation associated with several estimates is partially due to sampling error, we also made some biological assumptions. By removing the source populations we assumed that they were not contributing to this foraging area at levels sufficient to detect in this ML analysis. The nesting effort in NWFL may include 100–200 turtles annually (Meylan et al., 1995), as compared to tens of thousands of turtles that nest in southern Florida. Hence, the Florida panhandle is an important nesting area, but is probably too small to detect with precision in ML analyses. The removal of Greece as a potential source population was based on the results of the first analysis that indicated that this source population did not contribute at detectable levels (Table 1). Brazil was also removed from the analysis because there were no indications (either from the observed haplotypes or from the initial ML analysis) that this population contributed individuals to the foraging population at Hutchinson Island.

The results from the final ML analysis provided the most realistic estimate of the genetic composition of this area (Table 3). This analysis indicated that the SFL subpopulations is a major contributor to the Hutchinson Island foraging population. In addition, the Yucatan nesting population also appears to contribute a significant percentage of individuals to this area. Although the small northeast Florida to North Carolina (NEFL-NC) rookery appears to contribute some individuals, the standard error is still large; therefore, the estimate is not precise. Individuals from the NEFL-NC nesting population are present, but an accurate estimate (finer than 7–12%) is not possible at this time.

The results of the analysis of the St. Lucie foraging population are provisional and there are several limitations to the maximum likelihood analysis. A major assumption of this type of analysis is that all potential source populations

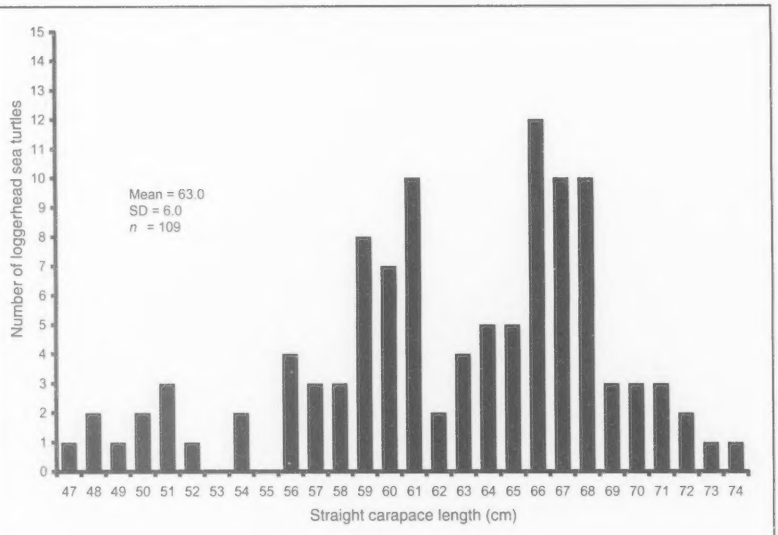

Figure 2

Length-frequency distribution for immature loggerhead sea turtles captured at the Hutchinson Island foraging ground (1999).

have been identified (Pella and Milner, 1987). Although the source population data set represents most of the major nesting colonies in the Atlantic, other nesting colonies exist that may contribute individuals to this foraging ground assemblage. For example, there are small nesting loggerhead populations on the Cape Verde Islands, Cuba, and on the coast of Colombia for which data are not accessible and we have been unable to estimate their possible contributions. If these nesting populations were included in the analysis there is a chance that the relative contributions of the source populations included in our study could be altered. A second major assumption is that the source populations were sampled sufficiently to uncover all haplotypes (Pella and Milner, 1987). In the case of the south Florida nesting assemblage, this assumption may not hold. As previously mentioned, south Florida supports the largest nesting assemblage in the Atlantic Ocean and it is possible that all haplotypes of the assemblage have not been determined. As with the inclusion of more potential source populations, there is the chance that changes in the frequency and distribution of haplotypes could alter the relative contributions reported in our study. We see these results as a sound starting point for the eventual analysis of foraging loggerhead sea turtles along the coast of the eastern United States.

The mean length of the 109 sampled turtles was 63.3 cm (SCL) with a standard deviation of 6.0 cm (Fig. 2). The mean lengths for all haplotype groups were very similar: for haplotypes A, B, C, and G (south Florida), mean length was 62.9 cm (±6.2); for haplotypes I and J (Yucatan), it was 63.8 cm (±8.0); and for haplotypes K, M, and N (other), it was 63.7 cm (±3.8).

Discussion

Although the estimates of percent contributions of the source populations generated here are provisional (i.e. more sampling of loggerhead nesting subpopulations may eventually uncover previously unrecorded haplotypes), they indicate that sea turtles foraging in the nearshore waters of Hutchinson Island originate from at least three rookeries in the Northwest Atlantic: SFL (69%), Yucatan (20%), and NEFL-NC (10%). Although the majority of animals appear to originate from Florida nesting beaches, the maximum likelihood analysis indicates that a substantial proportion of the foraging juveniles are coming from the southern nesting population in the Yucatan. In addition, the northern population, comprising animals nesting on beaches from northeast Florida to North Carolina, also contributes a smaller percentage of individuals.

Sears et al. (1995) reported on the demographic composition of juvenile loggerhead sea turtles off Charleston, South Carolina, and Norrgard and Graves (1995) analyzed juvenile loggerhead sea turtles from Chesapeake Bay, Virginia. Restriction fragment length polymorphism (RFLP) analysis of mtDNA was used to identify the genotype of individuals in both studies. The data sets were used in conjunction with a geographic survey limited to nesting locations in the North Atlantic Ocean and Mediterranean Sea by Bowen et al. (1993) to estimate the composition of these two areas. The estimates of contribution by nesting populations to these foraging areas (Table 4) appear to differ from the results presented in the present study, particularly the large contributions from the NEFL-NC haplotype. This may either reflect real differences in haplotype composition,

Table 4

Demographic compositions of coastal juvenile loggerhead sea turtles from U.S. coastal foraging habitats by using RFLP analysis. *n* = number of turtles in sample. SFL = south Florida; NEFL-NC = northeast Florida to North Carolina.

Location	SFL	NEFL-NC	*n*	Literature source
Chesapeake Bay	0.64	0.36	62	Norrgard and Graves (1995)
South Carolina	0.50	0.50	33	Sears et al. (1995)

inadequate sample sizes or sampling errors, or possibly changes between year classes. However, the differences are undoubtedly an artifact and are more likely due to the poor resolution and small sample sizes of the RFLP studies.

Comparisons of estimates generated by using different methods are problematic for several reasons. Recently, Encalada et al. (1998) published the results of a survey of nesting locations using sequences from the control region of the mtDNA. This region exhibits a sixfold increase in divergence rates when compared to estimates of divergence based on RFLP analysis. More variation was detected and consequently more haplotypes were identified than previously in Bowen et al. (1993). Encalada et al. (1998) also included several other nesting subpopulations in the Atlantic Ocean, in particular nesting subpopulations in northwest Florida and the Yucatan of Mexico.

The manner and routes of dispersal of posthatchling loggerhead sea turtles from the Yucatan and NWFL are undoubtedly complex and probably follow the same dispersal scenarios as proposed for the Kemp's ridley sea turtle (*Lepidochelys kempii*) by Collard and Ogren (1990). These loggerhead turtles either stay in the Gulf of Mexico or are transported into the Atlantic by the Florida Current. Once in the Atlantic, they either stay on the Continental shelf area or are entrained in major current systems and are transported to the eastern Atlantic Ocean for an undetermined amount of time before presumably returning to western Atlantic coastal benthic habitats. The SFL and NEFL-NC rookeries are all situated near the western boundary of the Gulf Stream where the hatchlings are quickly transported away from beaches. Juvenile loggerhead sea turtles leave their pelagic habitat over a range of sizes, and presumably ages, depending on feeding success. This estimate size range (SCL) was from 25 to 60 cm (Carr, 1986, 1987; Martin et al., 1989; Musick and Limpus, 1997). Hays and Marsh (1997) deduced from drift studies that the pelagic phase ended "at least for some loggerheads in the north Atlantic" when they were around 50 cm. These postpelagic turtles are thought to become coastal benthic crustacean foragers (Musick and Limpus, 1997) and to move up and down the U.S. East Coast seasonally.

Movements of juvenile loggerhead sea turtles tagged at the St. Lucie Power Plant indicate that a substantial portion of these turtles appear to reside in the immediate vicinity of Hutchinson Island (M. Bresette, unpubl. data). However, a few turtles have been documented from as far north as North Carolina and as far south as Florida Bay in southwest Florida. Most recaptured juvenile loggerhead sea turtles were from the north and may indicate that Hutchinson Island is near the southern boundary of the seasonal migration (Ernest et. al., 1989). Relatively few southern movements were recorded to Florida Bay. Over 47% of 3142 turtles under 85 cm captured at the St. Lucie Power Plant were captured from January through April 1976–2000 (Fig. 3). Captures then tapered off until December, consistent with seasonal north and south movements as suggested for immature turtles at nearby Cape Canaveral (Henwood, 1987). There has previously been no tagging evidence to indicate movements of these immature turtles outside the continental United States, yet these mtDNA data indicate a large contribution from Mexico.

The Hutchinson Island juvenile loggerhead sea turtles settle into this important coastal habitat at the same size, and presumably age, whatever their genetic origins are. This finding indicates that this particular coastal habitat may be critical for several western Atlantic populations of juvenile sea turtles, both loggerhead and green.

Management implications

The NEFL-NC population is of particular interest to some U.S. conservation biologists because of an apparent decline in nesting females prior to 1990 (Turtle Expert Working Group, 2000). The goal of protecting these turtles while in various developmental habitats is extremely complex, particularly when they intermingle with large numbers of sea turtles from a healthy (large) breeding population (SFL), as well as with small (NWFL) and foreign populations (Yucatan). Management measures affecting immature loggerhead sea turtles in the east-central Florida foraging habitats need to take into account the contributions from other source populations that may not be as robust as that of the south Florida population. Specific measures will depend largely on the demographic composition of stranded turtles with known sources of mortality. The genetic compositions of juvenile loggerhead sea turtles that are impacted by disease, boat collisions, anthropogenic debris, channel dredging, and recreational and commercial fisheries need to be determined before resource managers can take appropriate action. Unfortunately it is difficult to determine specific causes of mortality from stranded individuals, and researchers are unable to accurately determine the activities that affect specific nesting aggregations. The conservative approach would be to regulate all known sources of mortality to immature coastal loggerhead sea turtles until more data become available through aggressive genetic sampling and necropsies of stranded animals.

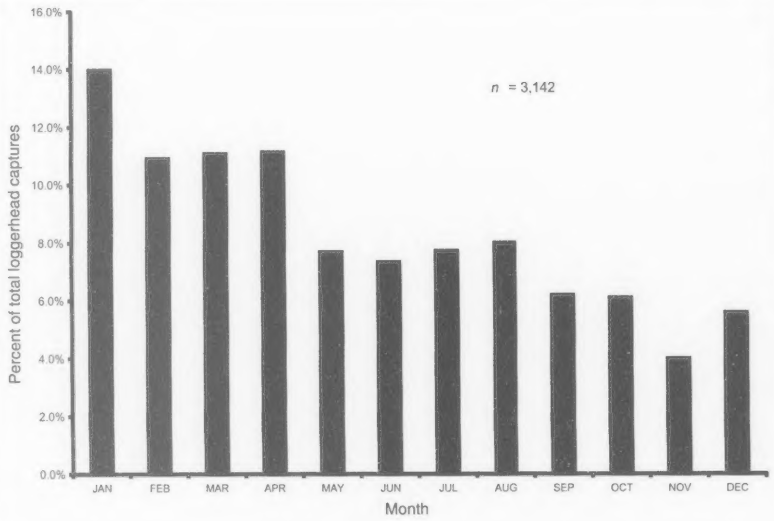

Figure 3

Monthly captures of loggerhead sea turtles less than 85 cm SCL at the St. Lucie Power Plant (1977–98).

The coastal foraging habitat near Hutchinson Island is also an important developmental habitat for endangered immature green sea turtles, *Chelonia mydas* (Bass and Witzell, 2000). This is a highly cosmopolitan species with contributions to the Florida foraging grounds from Costa Rica (53%), the United States and Mexico (42%), and Venezuela and Surinam (4%). It may be advisable for managers to designate specific areas, such as Hutchinson Island, as critical developmental habitats for immature sea turtles and to restrict public access.

The need for regional and internationally coordinated sea turtle research and management becomes obvious as genetic analysis reveals the complicated mixed stock of foraging turtle aggregations. International organizations, such as the International Union for the Conservation of Nature (IUCN) and the Intergovernmental Oceanographic Commission (IOCARIBE) need to become actively involved with the appropriate regional agencies of government to ensure the protection of sea turtle stocks in regional as well as international waters.

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Spawning of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) in the Mattaponi and Pamunkey Rivers, Virginia*

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In the Atlantic coastal region, American shad (*Alosa sapidissima*) is highly prized for its flesh and roe. Spawning runs have been heavily fished and since the late 1800s, landings have shown steady declines to the extent that Maryland declared a fishing moratorium in 1980, and Virginia followed in 1994 for Chesapeake Bay and its tributaries (ASMFC, 1999). Shad restoration projects are underway to restock depleted spawning runs, especially in regions where stream impediments have been or are being removed. Coastal ocean intercept gill-net fisheries have remained in place despite criticism and speculation about their impact on populations, particularly those river systems stocks that are depleted. The Atlantic States Marine Fisheries Commission Shad Board (ASMFC, 1999) adopted a fishery management plan for American shad and river herring that included a five-year phase-out of the ocean fishery and that required states to develop an approved fishing or recovery plan for each stock under restoration. In Virginia, this requirement applies to the James and York rivers.

Although the roe fishery for American shad has historically been important, there is little information about the specific spawning locations of these broadcast spawners. American shad are anadromous fish native to the Atlantic coast of North America, with a range extending from southeastern Labrador to the St. Johns River, Florida. In Chesapeake Bay tributaries, American shad deposit semidemersal eggs in the freshwater portions of the estuaries in the spring, usually beginning in March and ending by early June with peaks in April (Klauda et al., 1991). American shad have historically ascended farther upriver than at present, within tributaries where obstructions to movements upstream now exist. Prior to dam building in the 1800s on the James River, large numbers of American shad traveled over 335 miles from Chesapeake Bay into the Jackson and Cowpasture rivers (Mansueti and Kolb, 1953).

The York River, a coastal plain tributary located in the Chesapeake Bay watershed, is formed by the confluence of the Pamunkey and Mattaponi Rivers at West Point (Fig. 1). The Pamunkey River has a larger watershed (3768 km^2) and average spring discharge rate (47.5 m^3/s) than the Mattaponi River (2274 km^2; 27.2 m^3/s, respectively). Watershed sizes are based on U.S, Geological Survey digital line graph data (DLG) at 1:100,000. On these unobstructed rivers, annual releases of hatchery-reared American shad approximate two to four million fry through efforts of the Virginia Game and Inland Fisheries (VGIF) and an estimated 2.5 to 3 million fry are released by the Pamunkey tribal government. In addition there are unknown contributions from the Mattaponi tribal government (Gunther[1]). Current monitoring of adult catches indicates that the York River supports the strongest runs of shad in Virginia (Olney and Hoenig[2]). American shad in the York River are used as the source stock for hatchery efforts in the James and Potomac rivers. Thus, the restoration efforts in Virginia are dependent on the productivity of the York River.

Within the freshwater tidal portions of the Mattaponi and Pamunkey rivers, numerous other species spawn, including striped bass (*Morone saxatilis*) (McGovern and Olney, 1988; Grant and Olney, 1991). The Chesapeake Bay stock has rebounded after severe declines in the 1970s and early 1980s as a result of successful management and several years of successful reproduction (Olney et al., 1991; Field, 1997). The extent of the spawning area for both American shad and striped bass is in part a function of salinity and temperature. Striped bass spawn from the limit of brackish water to freshwater in the rivers of Chesapeake Bay from early April through the end of May (Setzler-Hamilton et al., 1981), and American shad spawn in freshwater (Leim, 1924). McGovern and Olney (1996) noted that the lower limit of striped bass spawning followed the 1 ppt salinity contour, and Secor and Houde (1995) postulated that the freshwater-saltwater interface may act as a down-river barrier to striped bass egg and larval advection. Based on suitable temperature ranges (12–24°C for striped bass [Setzler-Hamilton et al., 1980; Rutherford and Houde, 1995] and 12–25°C for Ameri-

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[1] Gunther, T. 2000. Personal commun. Virginia Game and Inland Fisheries, Richmond, Virginia 23230.

[2] Olney, J. E., and J. M. Hoenig. 2000. Monitoring relative abundance of American shad in Virginia's Rivers. March 1998–1999. Final report to the U.S. Fish and Wildlife Service and Virginia Marine Resources Commission, 53 p. Contract number F-116-R-1. Virginia Institute of Marine Science, Gloucester Point, Virginia.

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Figure 1

Extent of ichthyoplankton sampling by bongo net and pushnet in the Mattaponi and Pamunkey rivers (1997–99). Stations are denoted as the number of kilometers from the mouth of the York River.

can shad [Leach and Houde, 1999; Walburg and Nichols[3]] and salinity requirements for the early life stages of these species, the potential for spawning overlap spatially and temporally is high. Species interactions, including predation and competition by both adults and young, may play a role in the spawning and recruitment success of these species. Similar interactions have been postulated between American shad and other alosines in the Hudson River (Schmidt et al., 1988).

Our objectives were to describe the American shad spawning reaches in the Mattaponi and Pamunkey Rivers spatiotemporally, and to determine if striped bass also spawn within the identified spawning habitat of American shad. In year one, we completed an exploratory survey to map the distribution of the American shad spawning ground and the occurrence of striped bass within these reaches. In years two and three, sampling was modified to locate the upper limit of American shad and striped bass spawning within the two rivers.

Materials and methods

Sampling protocol in 1997

Exploratory sampling in the Mattaponi and Pamunkey rivers for eggs and larvae of American shad and striped bass extended from March through April 1997. Sites were chosen on the basis of a prior survey of American shad eggs in the rivers (Massmann, 1952). Sampling protocol included weekly ichthyoplankton collections during daylight hours with stepped oblique tows of a bongo frame fitted with two 333-µm mesh nets (60-cm diameter). Catches from both nets were combined. The same ten stations were sampled weekly on each river within the tidal freshwater reaches. Stations are depicted as river kilometers (rkm) from the mouth of the York River, for example, M68 is a station on the Mattaponi River that is approximately 68 river kilometers from the mouth of the York River. The stations were located at approximately 3.2-rkm intervals within the range of 72 to 106 rkm (P72 to P106) on the Pamunkey River and 68 to 102 rkm (M68 to M102) on the Mattaponi River (Fig. 1).

Sampling protocol in 1998 and 1999

In 1998 and 1999, station locations were extended upriver to include more shallow stations owing to the low abun-

[3] Walburg, C. H., and P R. Nichols. 1967. Biology and management of the American shad and the status of the fisheries, Atlantic coast of the United States, 1960. U.S. Fish and Wildlife Service, Special Scientific Report–Fish 550, 105 p. Fish and Wildlife Service, U.S. Dep. of Interior, Washington, DC 20005.

dance of American shad eggs in 1997. Bongo nets could not be used, and sampling included pushnet surveys in the upper reaches of the rivers (from 31 March through 20 May 1998 and from 11 April through 7 May 1999). The weekly sampling on each river consisted of pushnet tows at approximately one meter below the surface at each station. A pushnet frame fitted to the bow of a 14-foot boat (Olney and Boehlert, 1988) accommodated two plankton nets (333 µm, 60 cm). Catches from both nets were combined. In 1998, eight stations per river were systematically sampled bracketing M94 to M120 and P109 to P131. In 1999, two stations at M124 and M128 were added on the Mattaponi River; we added six upriver stations (P135–P154) and one downriver station (P104) on the Pamunkey River (each spaced at 3.2-rkm intervals, Fig. 1). Bongo and push nets were fitted with a flow meter for volumetric measurements and tow times were adjusted (three to seven minutes) to meet a lower limit of 50 m^3 of water filtered through both nets combined.

Laboratory procedures and data analysis

Ichthyoplankton samples were preserved in 10% phosphate-buffered formalin. Ichthyoplankton were sorted and larval fish and eggs were identified (Lippson and Moran, 1974; Jones et al.[4]), enumerated, and removed from the original, whole sample. Densities were reported as number per 100 m^3. Relative abundance in both rivers was calculated by average density of each life stage (egg, yolksac larva, and postyolksac) multiplied by total volume of spawning or nursery area sampled. Total volume of spawning or nursery area sampled was determined separately for each species by including locations within the sampling region where eggs (spawning reaches) or larvae (nursery reaches) were collected. River volumes were calculated by using bathymetric surveys and corresponding areal estimates from a digitized record of the mean high-water shoreline position as shown on the 7.5 minute topographic map series of the U.S. Geological Survey completed by Comprehensive Coastal Inventory, Virginia Institute of Marine Science (Bilkovic, 2000). For purposes of comparison, we used data on the abundance of American shad and striped bass juveniles in the Pamunkey and Mattaponi rivers. The data were taken from annual surveys of juvenile abundance conducted by the Virginia Institute of Marine Science (Austin et al., 2000; Olney and Hoenig[2]).

Results

Trends in density (numbers/100 m^3) of eggs for each river and species by date and station are depicted for 1997–99 in Figures 2 and 3. Average density (total eggs or larvae per total volume filtered) of each species per river is depicted in Figure 4. On the Mattaponi River (1997–99), American shad eggs were collected over a 44-km reach (M81–M124) and the highest densities occurred between M96 and M124. Striped bass spawning occurred over a 27-km reach and the highest densities in the sampled area occurred between M68 and M87, downstream of the primary spawning reaches of American shad (Figs. 2–4). On the Pamunkey River, American shad eggs were collected over a 53-km reach (P98–P150), and the highest densities were found between P104 and P131. Striped bass spawning occurred over a 60-km reach (P72–P131), and the highest densities were found between P72 and P87. There was some spatial overlap in spawning of these species, but the primary spawning reaches were separate. Temporal overlap in spawning of American shad and striped bass occurred throughout the sampled period in both rivers (Figs. 2–3).

On the Mattaponi River, American shad larvae (total length, 6.1–19.2 mm) were collected from M68 to M124, and the highest densities were observed between M94 and M102—a reach that is downstream of the spawning habitat. On the Pamunkey River, American shad larvae (total length, 6.6–12.2 mm) were collected between P76 and P128. Densities were highest at P102, 105, and 124. Larval striped bass were collected from M68 to M94 and from P72 to P109, and peak catches (>1/m^3) were collected from M68 to M80 and from P72 to P91. In both rivers, we observed overlap in American shad nursery grounds and striped bass spawning reaches. However, the highest densities of larval striped bass were downstream of the primary shad spawning and nursery areas (Fig. 4).

Average density of individual life stages of American shad was higher in the Mattaponi River than in the Pamunkey River; the opposite pattern was apparent for striped bass (Table 1). Estimates of the relative numbers of American shad and striped bass (average density × river volume) suggested that abundance of American shad eggs and larvae was higher on the Mattaponi River than on the Pamunkey River by a factor of 5.5 and 4.4, respectively. Relative abundance of striped bass eggs and larvae was higher on the Pamunkey River than on the Mattaponi River by a factor of 29 and 9.9, respectively (Table 2).

Discussion

Over the three years of surveys, eggs and larvae of American shad were rare compared to those of striped bass (Table 1). Despite our successive efforts to relocate sampling stations upstream of known striped bass spawning habitat (Grant and Olney, 1991; Olney et al., 1991), striped bass eggs and larvae were more abundant (~114 times and ~38 times, respectively) than those of American shad (Table 2). These differences could be attributed to the relative sizes and egg production of the spawning stocks because the number of mature American shad presently in the York River system is believed to be low in relation to historic run sizes (Nichols and Massmann, 1963; Olney

[4] Jones, P. W., F. D. Martin, and J. D. Hardy Jr. 1978. Development of fishes of the mid-Atlantic Bight. An atlas of egg, larval, and juvenile stages. Vol. 1, Acipenseridae through Ictaluridae. U.S. Fish and Wildlife Service report FSW/OBS-78/12. Fish and Wildlife Service, U.S. Dep. Commer., Washington DC 20005.

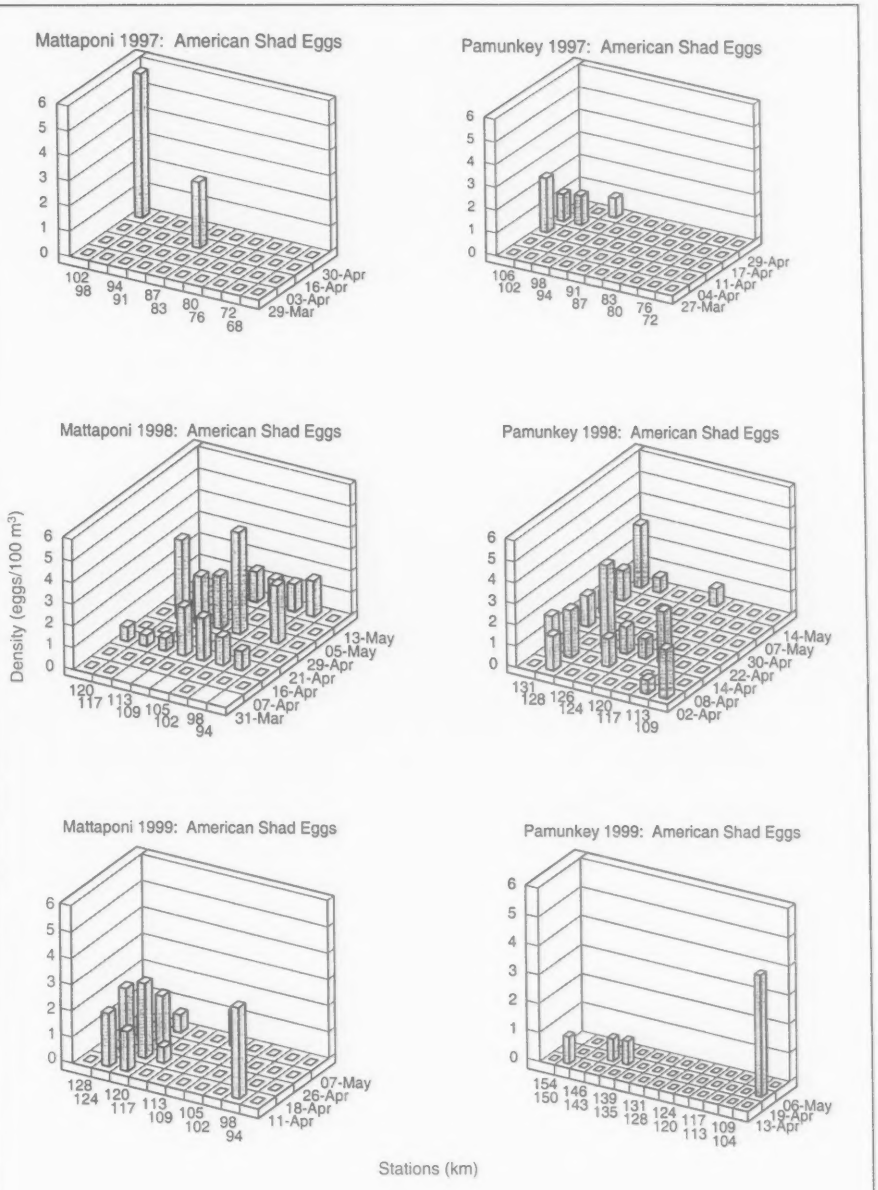
Mattaponi 1997: American Shad Eggs
Pamunkey 1997: American Shad Eggs
Mattaponi 1998: American Shad Eggs
Pamunkey 1998: American Shad Eggs
Mattaponi 1999: American Shad Eggs
Pamunkey 1999: American Shad Eggs
Density (eggs/100 m³)
Stations (km)

Figure 2

American shad egg density and distributions for 1997–99 bongo and pushnet collections. Stations are denoted as their distance (in kilometers) from the mouth of the York River.

and Hoenig[2]). In contrast, striped bass stocks are at record levels of abundance (Field, 1997) and support a large recreational and commercial fishery in the York River.

Despite the proximity and resemblance of the Pamunkey and Mattaponi Rivers, patterns of spawning and recruitment of American shad and striped bass are opposite for each tributary. We observed annual differences in abundance of eggs and larvae of these species that are concordant with indices of juvenile production. In our surveys, eggs and larvae of American shad were more abundant on the Mattaponi River and striped bass eggs and larvae were more abundant on the Pamunkey River (Tables 1 and 2). Similarly, mean recruitment (the mean index of juvenile abundance or JAI) of American shad

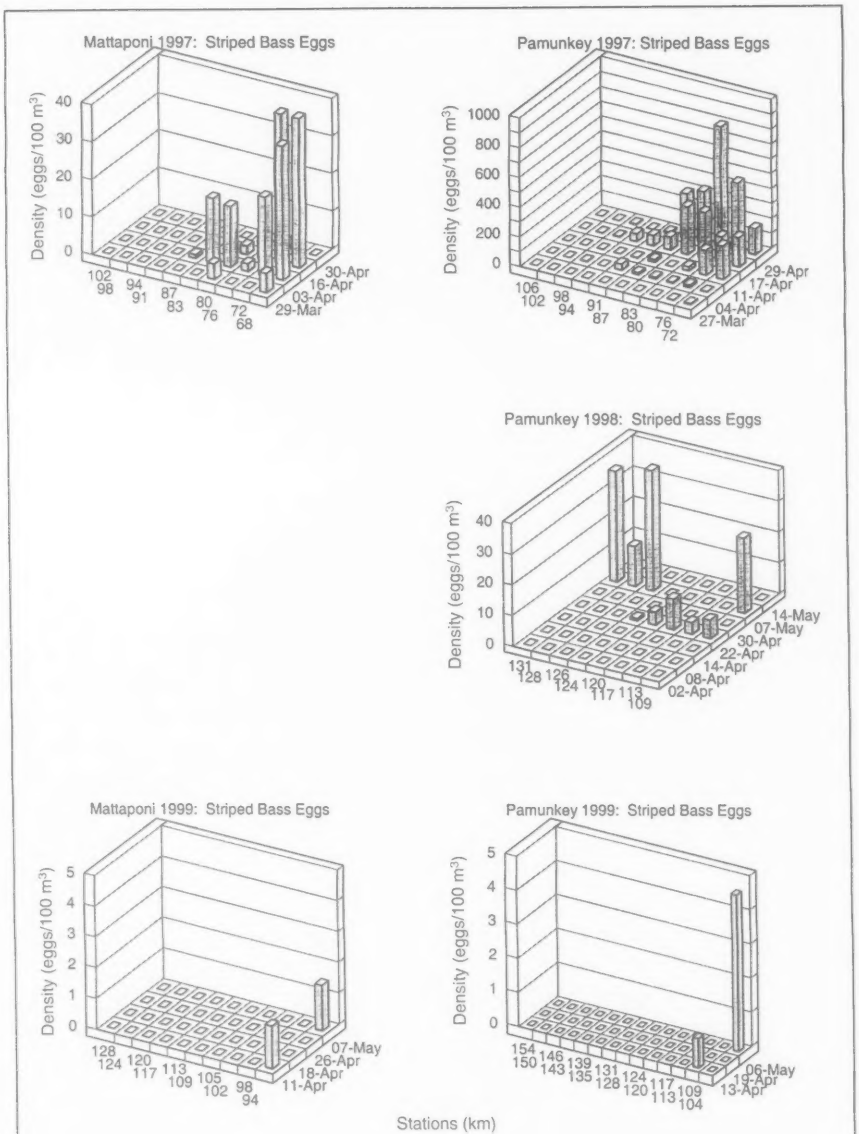

Figure 3

Striped bass egg density and distributions for 1997–99 bongo and pushnet collections. Stations are denoted as their distance (in kilometers) from the mouth of the York River. In 1998, no striped bass eggs were collected on the Mattaponi River.

was higher on the Mattaponi River (1997–99; Mattaponi JAI, 1648.5; Pamunkey JAI, 112.7), and mean recruitment of striped bass was higher on the Pamunkey River (1997–99; Mattaponi JAI, 1.6; Pamunkey JAI, 4.9). The approximate volume of the Pamunkey River, from the fall line to river mouth (1.9×10^8 m^3) is 1.2 times that of the Mattaponi River (1.6×10^8 m^3). Thus, equal populations of eggs or larvae that are homogeneously distributed on each tributary would be expected to be at the most 1.2 times as concentrated on the Mattaponi River. Because we observed differences in egg density that were much greater than double (~17 times in the case of striped bass) and in the unexpected direction (Pamunkey River egg densities > Mattaponi River egg densities), it is unlikely that

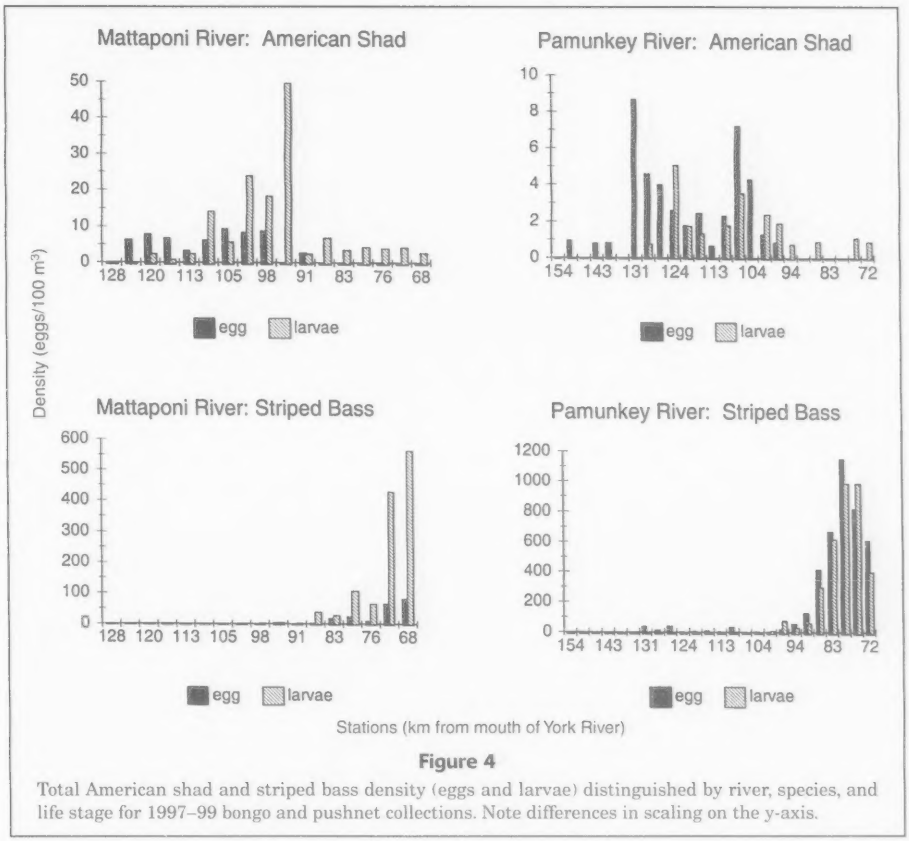

Figure 4

Total American shad and striped bass density (eggs and larvae) distinguished by river, species, and life stage for 1997–99 bongo and pushnet collections. Note differences in scaling on the y-axis.

Table 1

Average density (total numbers/total volume filtered) of eggs and larvae of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) collected in the Mattaponi and Pamunkey rivers, Virginia (1997–99). Values are reported as numbers per 100 m^3.

			Larvae		
Species	River	Eggs	Yolksac	Postyolksac	Total larvae
American shad	Mattaponi	59.1	32.8	67.3	100.1
	Pamunkey	33.7	11.5	6.2	17.6
Striped bass	Mattaponi	205.3	392.1	792.4	1184.5
	Pamunkey	4016.5	2625.9	909.8	3535.7

tributary volume alone is responsible for the contrasting patterns. Instead, differences in discharge, river sinuosity, habitat, stock size, or combinations of these factors may be responsible.

Temporal and spatial overlap in spawning distributions of American shad and striped bass occurs in the York River system but the primary spawning grounds of these species are disjunct. Evidence of spawning and peak egg abundance for both species was apparent throughout the water temperature range of 13–19°C in both rivers. Trends of general abundance for both years and rivers indicated that American shad spawn in regions upstream of striped bass primary spawning grounds (Fig. 4). Trophic interactions, especially predation and competition, may explain the disjunct spawning habitats of these species in the York River. Striped bass may be important predators on American shad in freshwater (Mansueti and Kolb, 1953; Walburg and Nichols[3]). Although recent studies have failed to detect

Table 2

Relative abundance (average density × river volume, numbers × 10^8) and ratios of eggs and larvae of American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*) collected in the Mattaponi and Pamunkey rivers, Virginia (1997–99). River volume (10^7 m^3) consists of reaches where eggs (spawning reaches) or larvae (nursery reaches) were found.

	River volume			Larvae		
Species	Spawning reaches	Nursery reaches	Eggs	Yolksac	Postyolksac	Total larvae
American shad						
Mattaponi	6.1	9.4	0.36	0.27	0.63	0.94
Pamunkey	1.9	12.0	0.07	0.13	0.07	0.21
Mattaponi: Pamunkey	3.2	0.8	5.5	2.0	8.8	4.6
Striped bass						
Mattaponi	7.9	3.3	1.6	1.3	2.6	4.0
Pamunkey	12.0	11.0	47.0	29.0	10.0	39.0
Pamunkey: Mattaponi	1.5	3.3	29.0	22.3	3.8	9.9

American shad in the diets of striped bass (Manooch, 1973; Austin and Walter[5]), this absence may be due to current low numbers of American shad in relation to other clupeids. Correspondingly, American shad juveniles have the potential to prey upon striped bass larvae (McGovern and Olney, 1988). Competition for food may occur between the early life stages of these two species as well. According to several studies, larval and juvenile stages of striped bass and American shad feed on similar prey items (Massmann, 1963; Markle and Grant, 1970; Setzler-Hamilton et al., 1981; Gardinier and Hoff, 1982; Crecco and Blake, 1983; Johnson and Dropkin, 1997; Ross et al., 1997). Distinct spawning locations of these species may act to minimize competition between larval- and early juvenile-stage fish, which use nursery locations downriver of spawning reaches. There is also potential overlap in habitat use between the juveniles of these species because both species occupy shallow nearshore waters. Some habitat overlap may be avoided by differing inshore-offshore diel migration patterns. American shad occupy nearshore areas during daylight and move offshore during night hours (Schmidt et al., 1988), whereas striped bass have been observed to predominately occupy nearshore habitats during both day and night hours (Boynton et al., 1981; Rudershausen and Loesch, 2000).

Locations of striped bass spawning grounds on the Pamunkey River in this study corresponded to those of previous studies. Primary spawning reaches on the Pamunkey River were previously reported from 8–48 km above West Point (Rinaldo, 1971); at approximately 27 km (Pamunkey) and 14 km (Mattaponi) above the mouth of each river (Tresselt, 1952); and within the first 40 km of tidal freshwater of both rivers (Grant and Olney, 1991). In the our study, some striped bass eggs were collected on the Pamunkey River upstream of previously reported locations, but in lower abundance than occurred downstream. In the Mattaponi River, striped bass eggs were absent in upstream locations, an observation in agreement with previous surveys (Tresselt, 1952; Rinaldo, 1971; Grant and Olney, 1991; McGovern and Olney, 1996).

On both rivers, American shad were collected in higher abundance upriver of previously reported primary ranges by Massmann (1952). He observed peak egg abundance from 96.2 to 111.0 rkm on the Pamunkey River and from 81.4 to 94.4 rkm on the Mattaponi River. This is in part because we sampled farther upriver than Massmann. However, in those upriver reaches that both studies sampled, eggs were found in higher abundance in 1997–99. Shifting spawning habitats (possibly due to changes in population structure and size, climate, or river discharge), sampling deficiencies, unknown catchability differences between the studies, or some combination of these factors may explain these historical differences. As populations of American shad fluctuate, the spawning area used will likely expand or shrink. If restoration efforts are successful, the availability of suitable spawning areas may become a limiting factor to population growth. Further studies of habitat suitability for spawning within this system are underway to elucidate potential spawning reaches and optimal areas.

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[5] Austin, H. M., and J. F. Walter. 1998. Food habits of large striped bass in the lower Chesapeake Bay and its tributaries March 1997–May 1998. Final report to the Marine Recreational Fisheries Advisory Board and Commercial Fisheries Advisory Board, VMRC, 56 p. Contract number RF-97-08 and CF09709-08. Virginia Institute of Marine Science, Gloucester Point, VA 23062.

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Spawning, growth, and overwintering size of searobins (Triglidae: *Prionotus carolinus* and *P. evolans*)*

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The northern searobin, *Prionotus carolinus*, and striped searobin, *P. evolans*, are among the most common benthic fishes of continental shelf waters between Cape Cod and Cape Hatteras, and both species have contributed occasionally to landings of the U.S. middle Atlantic states. Although several life history studies of these species have been published (Marshall, 1946; Wong, 1968; McEachran and Davis, 1970; Richards et al., 1979; McBride et al., 1998), their early life history has been poorly documented until recently (McBride and Able, 1994; Able and Fahay, 1998; McBride et al., 2002). Obstacles to early life history studies of these searobins include the following: 1) eggs and preflexion larvae are difficult to identify; 2) spawning occurs concurrently for several months; 3) slow growth rates confound analysis of size frequencies for determining cohort structure, and 4) conventional sampling methods have provided few late-stage larvae and early juveniles. I set out to avoid these problems by collecting juvenile specimens from the field and analyzing their otolith microincrements to determine spawning periodicity and growth rates. This approach has not previously been applied to any triglid (Secor et al., 1992).

This study demonstrates both interspecific and intraspecific differences in size during the first year. A literature review also suggests that age-0 *P. carolinus* are smaller than age-0 *P. evolans* and that conspecifics at northern latitudes are larger than conspecifics at southern latitudes (Table 1). In this study, daily sagittal micro-increments were validated and used to test whether interspecific spawning date differences, growth rate differences, or both, are responsible for size differences at first winter. Size at first annulus formation was also examined as an independent measure of age and growth rate. The results of this study improve our understanding of the continental shelf as a nursery ground and the geographic variation in life history traits for these two species.

Materials and methods

Otolith micro-increment validation

Otolith ontogeny was examined by using cultured embryos and yolksac larvae. *Prionotus carolinus* eggs were collected from ripe adults in August 1992 in coastal waters and fertilized in the laboratory. Embryos were raised in 10-liter aquaria under a 12:12 hour light:dark cycle, at 31 ppt salinity, and 26°C. Cultured *P. carolinus* embryos began to hatch after 48 hours and nearly all fish had hatched by 56 hours. Laboratory temperatures unintentionally dropped to 22°C after hatching, but no mortality was observed. Embryos and larvae were preserved in 95% ETOH at 8–16 hour intervals for the first three days and 22–26 hours for the following three days. No fish survived beyond six days. No water was exchanged, but constant aeration kept the aquaria well mixed during the experiment. Newly hatched *Artemia* sp. nauplii were supplied to yolksac larvae, but no feeding was observed. All mortalities appeared to be caused by starvation.

Embryos or larvae were placed on a slide under a cover slip or set in immersion oil (Secor et al., 1992) to examine otolith ontogeny. Otolith presence, size, and development were noted with both a binocular scope (≤50×) and a compound microscope (40–1000×) with polarized light. Notochord length (NL) was measured with an ocular micrometer to the nearest 0.1 mm. Otoliths were measured from a digitized video image through a compound microscope to the nearest 0.001 mm.

Field-collected *P. carolinus* juveniles were chemically marked with tetracycline, held in the laboratory under controlled conditions, and the relationship between "days captive" and "rings after the tetracycline mark" was tested against a 1:1 ratio. Newly settled *P. carolinus* (10–15 mm standard length [SL]) were collected near Beach Haven Ridge (New Jersey) by using a 1- or 2-m beam trawl on five different dates in October 1992 (see McBride et al. [2002] for sampling locations). These fish were divided into four replicate groups; each group was marked separately with a solution of oxytetracycline (dihydrate) and ambient seawater (a concentration of 500 mg/L; 26–28 ppt; 20–22°C) for 24 hours.

One 40-liter aquarium per replicate group was maintained as a flow-through (about 1–10 mL/s) system. Daily water temperature averaged 20.6°C (±2.7 SD), salinity averaged 28.5 ppt (±1.4) and the photoperiod was 12:12 hours of light:dark. Tetracycline-marked fish were fed thawed *Artemia* sp. 2–4 times daily, and a sup-

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Table 1

Standard length (mm) at age for *Prionotus carolinus* and *P. evolans* from two different geographic regions. Fishes older than age 6 are not included because they were typically represented by only individual fishes. nd = no data.

	Chesapeake		New England	
Age (yr)	*P. carolinus*[1]	*P. evolans*[2]	*P. carolinus*[3]	*P. evolans*[3]
0	nd	nd	75	90
1	126	132	130	160
2	163	186	195	210
3	180	207	220	235
4	197	224	245	260
5	204	245	255	290
6	211	270	270	305

[1] Average length values converted from fork length using equations in Wong (1968; Tables 2 and 3).
[2] Values are medians converted from fork lengths as reported in McEachran and Davis (1970, p. 347–348).
[3] Values estimated as a median from Richards et al. (1979; Fig. 7).

plemental feed with vitamins and oils was given at least once each week. Their ration was approximately 10% of their body weight/day; this ration was adjusted 1–3 times weekly to reflect the changes in weight during the experiment. Uneaten food was removed daily. Three to seven fish were removed from each replicate aquarium after 16, 26, 36, 46 days (total n=75), measured to the nearest 0.1 mm SL, and preserved in 95% ETOH. Growth rates between the replicate tanks varied from 0.21 to 0.44 mm/d according to least squares, linear regression of standard length on date of removal. Eleven of 86 fish initially placed in the aquaria died during the experiment and were not used for validating microincrement deposition rate.

After preservation, both sagittae were extracted from each fish, mounted on a coded glass slide in nail polish, sanded along the sagittal plane, and swabbed with immersion oil. After a fluorescing increment was located in the ocular crosshairs using a ultraviolet light source, the light was turned off and I counted the microincrements from the crosshair to the otolith margin on three separate dates. An average of these three counts was used to estimate increment number from the tetracycline mark to the peripheral edge.

Daily age and growth

Sagittal microincrements were examined from other postsettlement *P. carolinus* and *P. evolans* juveniles collected during August–October 1991 at locations in Great Bay (New Jersey), Delaware Bay, and continental shelf sites between Chesapeake Bay and Long Island Sound. Fishes were collected with bottom trawls and seine nets and either preserved in 95% ETOH or frozen. Specimens for aging were subsampled in a stratified (1-mm length category) random manner to proportionally represent the complete size range of each independent sample.

Otoliths were mounted on coded slides in nail polish and sanded to the core along one side of the sagittal plane or embedded in an epoxy resin and sectioned to the core (Secor et al., 1992). I counted microincrements through a compound microscope, typically at 400× by using polarized light, on three separate occasions. If the range of all three counts was >20% of the mean count, then the specimen was excluded from further analyses; this criterium resulted in 14 of 137 specimens being rejected. The mean increment count for sagittae was used to estimate "otolith age" in days. Daily age included four additional days—an estimate of the time between hatching and the date of first ring deposition. Hatching dates were calculated by subtracting daily age from date of capture.

Annual age and growth

Size attained by the end of the first growing season was estimated from *P. carolinus* and *P. evolans* juveniles collected during later winter and early spring cruises by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (see also McBride et al., 1998). Fishes were sampled with bottom trawls during two consecutive cruises (February 1993 and March–April 1993), which included a total of 447 stations (Fig. 1). The effective period of sampling for searobins was actually February–March (only one searobin was caught in 160 tows made during April).

At sea, only fishes ≤120 mm SL were saved because larger fishes were presumed to be older than 1 year (see Richards et al., 1979). Fishes were kept frozen to preserve the otolith structure. Specimens were subsampled from each independent sample (i.e. tow) in a stratified (5-mm length intervals), random manner. This subsampling approach was chosen again to moderate the resulting sample size while proportionally representing the complete size range of each independent sample; this approach also exaggerates the size range by dampening the modes of resulting size-frequency data. Sagittae were mounted in nail polish on a coded glass slide, sanded, and polished along

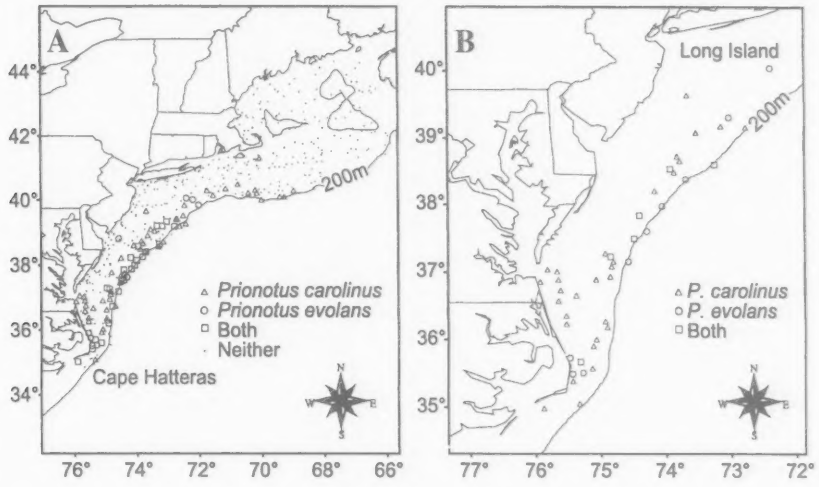

Figure 1

(**A**) Locations of all sampling during February–April 1993. Locations are indicated where searobins were and were not collected in tows. (**B**) Sample locations for age-0 searobins used for estimating overwintering size. Locations are for cruise dates during February–March 1993. No age-0 *Prionotus* spp. were collected during April 1993, and sampling areas covered during April (north of 40°N) are not shown.

the sagittal plane, and viewed under a binocular scope (typically at 20×) to check for the presence (e.g. age-1) or absence (e.g. age-0) of an annulus. Annulus formation occurs in March for both species (Wong, 1968; McEachran and Davis, 1970), and an annulus on the otolith margin was not counted.

Results and discussion

Otolith microstructure

Two pairs of otoliths (the sagittae and lapilli) were present prior to hatching in cultured embryos, having formed at the same time as the optic vesicles. No asterisci were observed in cultured yolksac larvae and, from personal observations of field-caught specimens, the asterisci form after flexion of the notochord. First ring deposition in sagittae was contemporaneous with eye pigmentation and yolksac absorption, although this process was not observed directly. Instead, it was observed that the diameter of the sagittal core (=primordium) steadily increased during yolksac absorption but that no microincrements were evident. I conclude that the laboratory specimens would have laid down their first ring at yolk absorption had they survived because the diameters of their sagittae were similar to the sagittal core diameters of wild fish (i.e. the diameter of the first microincrement). The maximum sagittal diameter of laboratory-cultured *P. carolinus* larvae was 26.3 µm and the mean sagittal core diameter of field-caught fish was 27.0 or 26.8 µm (n=8 flexion stage and n=6 postflexion specimens, respectively).

Yolksac absorption occurred approximately six days after fertilization and four days after hatching at 22–26°C; therefore four days were added to the average number of microincrements counted for both species, although this developmental pattern was observed only for *P. carolinus*. The rate of larval development observed in the present study is consistent with other reports of *P. carolinus* cultured at 15–22°C. Yuschak and Lund (1984) observed yolksac absorption by *P. carolinus* larvae at 3.4 mm NL and first feeding at 3.5–5 days after hatching. Kuntz and Radcliffe (1917) reported *P. carolinus* hatching at about 60 hours (2.5 days) and starvation 5–6 days after hatching.

Sagittal microincrement deposition occurred daily in chemically marked *P. carolinus* juveniles cultured in the laboratory. Data from four replicate aquaria (75 fish) were pooled because an ANCOVA did not indicate a significant difference by either the interaction of treatments (slope–replicate interaction: P=0.48) or the covariate (replicate: P=0.12). The resulting relationship was

$$Y = 1.23 + 0.94\,(X),$$

where Y = the number of microincrements after the tetracycline mark; and
X = the number of days following marking.

A test of statistical power (i.e. 1 – beta, as in Dixon and Massey [1951] and Cohen and Cohen [1975]) indicated a 99.9% confidence that microincrement deposition did not deviate from unity by more than 0.02 rings/d. McBride (1994) presented preliminary evidence of daily sagittal microincrements in *P. evolans*.

Reproductive seasonality The reproductive period for both species was prolonged and overlapping (Fig. 2). The range of *P. carolinus* hatching dates was from 19 May to 5 September and *P. evolans* hatching dates extended from 2 June to 3 September. Median hatching dates for *P. carolinus* were significantly later than *P. evolans* (13 August versus 26 July; Wilcoxon 2-sample test: P=0.011). Both species spawned for at least three months but *P. carolinus* hatching dates were dramatically skewed to the left (i.e. most individuals hatched late in the season). Previous studies independently demonstrated that both species spawn contemporaneously in the New York Bight: Keirans et al. (1986) calculated egg densities, Wilk et al. (1990) examined gonadosomatic indices, McBride and Able (1994) used length-frequency analysis, and McBride et al. (2002) examined larval densities. All demonstrated an extended spawning season for both species from about May to September; furthermore, a bimodal pattern of spawning output was reported for *Prionotus* spp. by Keirans et al. (1986) and McBride and Able (1994). My sampling procedure (i.e. a stratified, random design with respect to length intervals) would flatten frequency peaks and emphasize the range of hatching dates, a method not well suited for identifying multiple spawning peaks. Moreover, McBride et al. (2002) identified notable geographic variation in spawning seasonality, which could not be separated out in the present study and should be accounted for in future research. Intra-annual reproductive periodicity of *Prionotus* should also be evaluated by examining gonads for cyclic, group-synchronous oocyte development, which could be an underlying process leading to a protracted spawning period with regularly spaced peaks in production.

I conclude that interspecific size differences are at least partly the result of interspecific differences in reproductive seasonality (Table 1; i.e. the smaller congener was spawned later in the year). However, Able and Fahay (1998) noted that *P. evolans* eggs are larger than *P. carolinus* eggs; thus size differences exist among embryos. In addition, McBride et al. (2002) showed that interspecific size-at-age differences are evident throughout the larval period.

Age and growth Age-0 *P. evolans* were larger at a common age than *P. carolinus* (Fig. 3). On the basis of all individuals examined, *P. evolans* did not grow at a significantly higher rate (ANCOVA interaction of slopes; P=0.099), but this species was significantly larger than *P. carolinus* in general (ANCOVA test of intercepts; P=0.0001). The regression slopes, based on all data, were significantly different from zero (P<0.001) for both *P. carolinus* (SL=0.12+0.323×*age*; r^2=0.62; n=70) and *P. evolans* (SL=3.52+0.429×*age*; r^2=0.53; n=53). The intercepts for these linear growth models were biologically meaningful, particularly that for *P. evolans* because the intercept was roughly equal to the known size at hatching (3 mm; Able and Fahay, 1998). *Prionotus evolans* collected at four different stations in Delaware Bay during October 1991 deviated strongly from the average growth rates for this species (Fig. 3). Such small, slow-growing fish demonstrated the degree of intraspecific variation possible for *P. evolans* growth rates.

Age-0 *P. carolinus* were also much smaller on average than *P. evolans* during winter (Fig. 4). By February–March, age-0 *P. carolinus* ranged from 27 to at least 117 mm SL, but this size distribution was strongly bimodal with modes at 42.5 mm and 87.5 mm SL. The age-0 *P. evolans* were all larger than 75 mm SL and appeared to grow even larger than 120 mm SL, which was the cutoff size for collections, so that the interspecific size difference is even greater than that indicated in Figure 4. Apparently all age-1 *P. evolans* are larger than this cutoff value because none were observed in the samples, whereas age-1 *P. carolinus* ranged from 56 to at least 118 mm. Although age-1 *P. carolinus* were generally larger than age-0 conspecifics, the sizes of both age classes overlapped in a manner that would confound length–frequency analyses of this species.

The intraspecific size variation of age-0 fishes, of both *Prionotus* species, was spatially correlated. Individually,

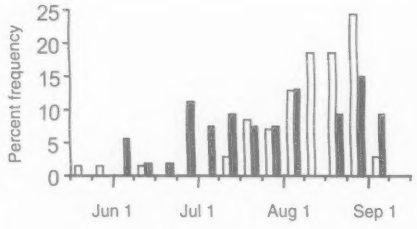

Figure 2

Backcalculated hatching dates (*date of capture* – [*otolith age* + 4]) for age-0 *Prionotus carolinus* (open bars; n=70) and *P. evolans* (filled bars; n=53) collected in estuarine and continental shelf habitats during 1991.

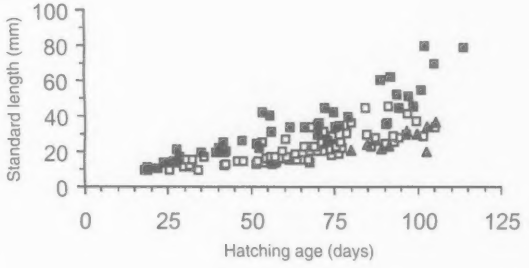

Figure 3

Length-at-age relationships for *Prionotus carolinus* (open symbols) and *P. evolans* (filled symbols). *Prionotus evolans* from Delaware Bay are depicted separately (triangles) from all other *P. evolans* (squares). Sample sizes are identical to those in Figure 2.

depth and latitude explained a significant ($r^2 \geq 0.30$; $P < 0.01$) amount of the variability of the mean size of age-0 *P. carolinus* during winter (Fig. 5). Each variable also contributed significantly ($P \leq 0.02$) to a multiple regression; nearly half ($r^2 = 0.47$) of the variance of the mean age-0 *P. carolinus* size between individual trawl tows was explained by the linear, least-squares equation

$$mean\ SL = -158 + 0.37 \times (depth[\text{m}]) + 5.7 \times (latitude[^\circ\text{N}]).$$

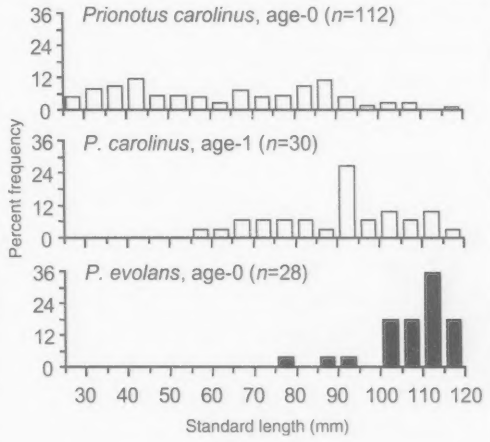

Figure 4

Size frequency of *Prionotus carolinus* (open bars) and *P. evolans* (filled bars) based on collections from continental shelf habitats in February–March 1993 (see Figure 1B). The upper boundary (120 mm SL) represents the size cutoff used during field collecting and does not necessarily define the maximum size attained for any age class. n = number of fish in sample.

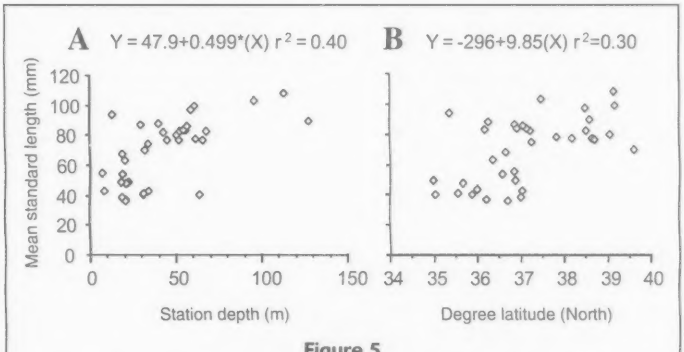

Figure 5

Linear relationships between mean size (standard length [mm]) of age-0 *Prionotus carolinus* and depth (**A**) or latitude (**B**) of sampling location. All fish were collected during February–March 1993 with bottom trawls in continental shelf waters (see Fig. 1B). See text for further details of multivariate analysis and results.

Similar analyses for *P. evolans* suggested that depth, but not latitude, was correlated with age-0 size variations. However, samples sizes of *P. evolans* were smaller than those for *P. carolinus* and age-0 *P. evolans* grow larger than the maximum size saved in field collections; therefore it is possible that age-0 *P. evolans* have a similar response to depth and latitude as age-0 *P. carolinus*.

Life history consequences

Late-summer spawning by *Prionotus* is not unique among fishes in waters offshore of the middle Atlantic states: *Scophthalmus aquosus* spawn late in the summer (Morse and Able, 1995) and three hake species (*Urophycis bilinearis*, *U. chuss*, and *U. regia*) have peaks in spawning during July–September (Wilk et al., 1990). Late spawning is not even evident for all *Prionotus* throughout their range. McBride et al. (2002) noted that the reproductive season for *Prionotus* varies with respect to latitude and coastal depth, and their observation that late spawning was common only offshore of the southern middle Atlantic states is consistent with the data presented in the present study for larger (i.e. presumably older) *P. carolinus* found during winter at higher latitudes. Sherman et al. (1984) noted a close association between *Prionotus* spawning cycles and zooplankton abundance cycles in continental shelf waters, and they suggested that the *Prionotus* spawning season is adapted for larvae to experience optimal prey encounter rates. However advantageous this match between larvae and their prey may seem, late-spawned *Prionotus* have an apparent size disadvantage during winter compared to many other species because of a shorter growing season.

Generally, coastal fishes of temperate waters appear to spawn in a manner that maximizes growth rates and size of their progeny, particularly in response to size-selective mortality (Conover, 1992; Sogard, 1997). Overwintering sizes of age-0 *P. carolinus*, however, do not suggest that such a scenario is occurring. Age-0 *P. carolinus* are smaller than or about the same size as typical age-0 prey species on the continental shelf, such as *Menidia menidia* and *Anchoa mitchilli* (Conover and Murawski, 1982; Vouglitois et al., 1987). Despite their small size, reports of age-0 *Prionotus* in gut contents of predatory fishes are rare (Marshall, 1946; Richards et al., 1979; Maurer and Bowman[1]). Size-selective mortality, a process that would select for early spawning and fast growth rates, may not be important because *Prionotus* are capable of burying themselves in the substrate (Bardach and Case, 1965)—an antipredator tactic. If size-selective mortality is not important, then

[1] Maurer, R. O., Jr., and R. E. Bowman. 1975. Food habits of marine fishes of the northwest Atlantic–data report. Laboratory Reference 75-3, 90 p. Northeast Fisheries Science Center. Woods Hole, MA 02543.

it is possible that overwinter mortality rates are similar between small individuals spawned late in the growing season and larger conspecifics spawned early, and that late spawning is not selected against for *P. carolinus*.

In this study, I demonstrate that interspecific and clinal variations of overwintering size for *Prionotus* species exist and that these are consistent with previous age and growth studies. Ginsburg (1950) also noted clinal variation for some meristic characters of both congeners that is consistent with Jordan's rule (i.e. higher counts at higher latitudes). McBride et al. (2002) have demonstrated regional differences in spawning seasonality for *Prionotus* species and short larval durations that limit dispersal of *Prionotus* planktonic stages; these are the likely mechanisms maintaining regional differences in juvenile sizes and meristic characters. Researchers should be aware of this demonstrated clinal variation and the potential for further life history, phenotypic, and possibly genetic variation of *Prionotus* species in temperate waters of the western North Atlantic.

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Errata

Erratum 1

Fishery Bulletin **100(2): 242.**

Kitada, Shuichi, and Kiyoshi Tezuka.

Longitudinal logbook survey designs for estimating recreational fishery catch, with application to ayu (*Plecoglosssus altivelis*)

Please note that in the printed copies some equations in Appendix 1 and Appendix 2 incorrectly show carets over the word "Cov."

Appendix 1 and Appendix 2 (page 242) should read as follows:

Appendix 1: The covariance of two estimators from sample means

First we consider the covariance of two total estimates. Let X_i and Y_i be simple random samples (i=1, . . . , n) from a population of size N with mean μ_x and μ_y, and $\overline{X}$ and $\overline{Y}$ be two sample means.

Cochran (1977, p .25) derived the covariance of two-sample mean, that is

$$\begin{aligned}\mathrm{Cov}(\overline{X},\overline{Y}) &= \frac{N-n}{N}\frac{1}{n}\mathrm{Cov}(X,Y)\\ &= \frac{N-n}{N^2 n}\sum_{i=1}^{N}(X_i-\mu_x)(Y_i-\mu_u).\end{aligned}$$

This is estimated by

$$\begin{aligned}\widehat{\mathrm{Cov}}(\overline{X},\overline{Y}) &= \frac{N-n}{N}\frac{1}{n}\widehat{\mathrm{Cov}}(X,Y)\\ &= \frac{N-n}{Nn(n-1)}\sum_{i=1}^{n}(X_i-\overline{X})(Y_i-\overline{Y}).\end{aligned}$$

The covariance between two population total estimators is defined by

$$\begin{aligned}\mathrm{Cov}(\hat{X},\hat{Y}) &= \mathrm{Cov}(N\overline{X},N\overline{Y}) = E(N\overline{X}-N\mu_x)(N\overline{Y}-N\mu_y)\\ &= N^2\mathrm{Cov}(\overline{X},\overline{Y}) = \frac{N(N-n)}{n}\mathrm{Cov}(X,Y).\end{aligned}$$

This is estimated by

$$\widehat{\mathrm{Cov}}(\hat{X},\hat{Y}) = \frac{N(N-n)}{n(n-1)}\sum_{i=1}^{n}(X_i-\overline{X})(Y_i-\overline{Y}).$$

For the monthly total catches, we get

$$\widehat{\mathrm{Cov}}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)}) = \frac{N(N-n)}{n(n-1)}\sum_{i=1}^{n}(C_{ik}-\hat{\overline{C}}_k)(C_{ik'}-\hat{\overline{C}}_{k'}).$$

Appendix 2: Approximate covariance between $\hat{W}_k^{(s)}$ and $\hat{W}_{k'}^{(s)}$

Taylor's series of $\hat{W}_k$ with respect to the random variables is obtained by

$$\hat{W}_k \simeq C_k\overline{w}_k + \overline{w}_k(\hat{C}_k - C_k) + C_k(\hat{\overline{w}}_k - \overline{w}_k).$$

From Taylor's series (mentioned above), the approximate covariance is obtained.

$$\begin{aligned}\mathrm{Cov}(\hat{W}_k^{(s)},\hat{W}_{k'}^{(s)}) &= E(\hat{W}_k^{(s)}-W_k^{(s)})(\hat{W}_{k'}^{(s)}-W_{k'}^{(s)})\\ &\simeq E\Big[\overline{w}_k(\hat{C}_k^{(s)}-C_k^{(s)}) + C_k^{(s)}(\hat{\overline{w}}_k-\overline{w}_k)\Big]\\ &\quad\Big[\overline{w}_{k'}(\hat{C}_{k'}^{(s)}-C_{k'}^{(s)}) + C_{k'}^{(s)}(\hat{\overline{w}}_{k'}-\overline{w}_{k'})\Big]\\ &= \overline{w}_k\overline{w}_{k'}\mathrm{Cov}(\hat{C}_k^{(s)},\hat{C}_{k'}^{(s)}) + \overline{w}_k C_{k'}^{(s)}\mathrm{Cov}(C_k^{(s)},\hat{\overline{w}}_{k'})\\ &\quad + C_k^{(s)}\overline{w}_{k'}\mathrm{Cov}(\hat{\overline{w}}_k,\hat{C}_{k'}^{(s)}) + C_k^{(s)}C_{k'}^{(s)}\mathrm{Cov}(\hat{\overline{w}}_k,\hat{\overline{w}}_{k'}).\end{aligned}$$

Here $\hat{C}_{(.)}^{(s)}$ and $\hat{\overline{w}}_{(.)}$ are independent, and both w_k and $w_{k'}$ are estimated from different samples. Therefore Cov $(\hat{C}_k^{(s)},\hat{\overline{w}}_{k'}) = \mathrm{Cov}(\hat{\overline{w}}_k,\hat{C}_{k'}^{(s)}) = \mathrm{Cov}(\hat{\overline{w}}_k,\hat{\overline{w}}_{k'}) = 0$, then we get the covariance as only the first term.

Erratum 2

Fishery Bulletin **100 (2):258.**

McFee, Wayne E., and Sally R. Hopkins-Murphy

Bottlenose dolphin (*Tursiops truncatus*) strandings in South Carolina, 1992–1996

Last sentence of abstract should read as follows:

Incidents of bottlenose dolphin rope entanglements accounted for 16 of these cases.

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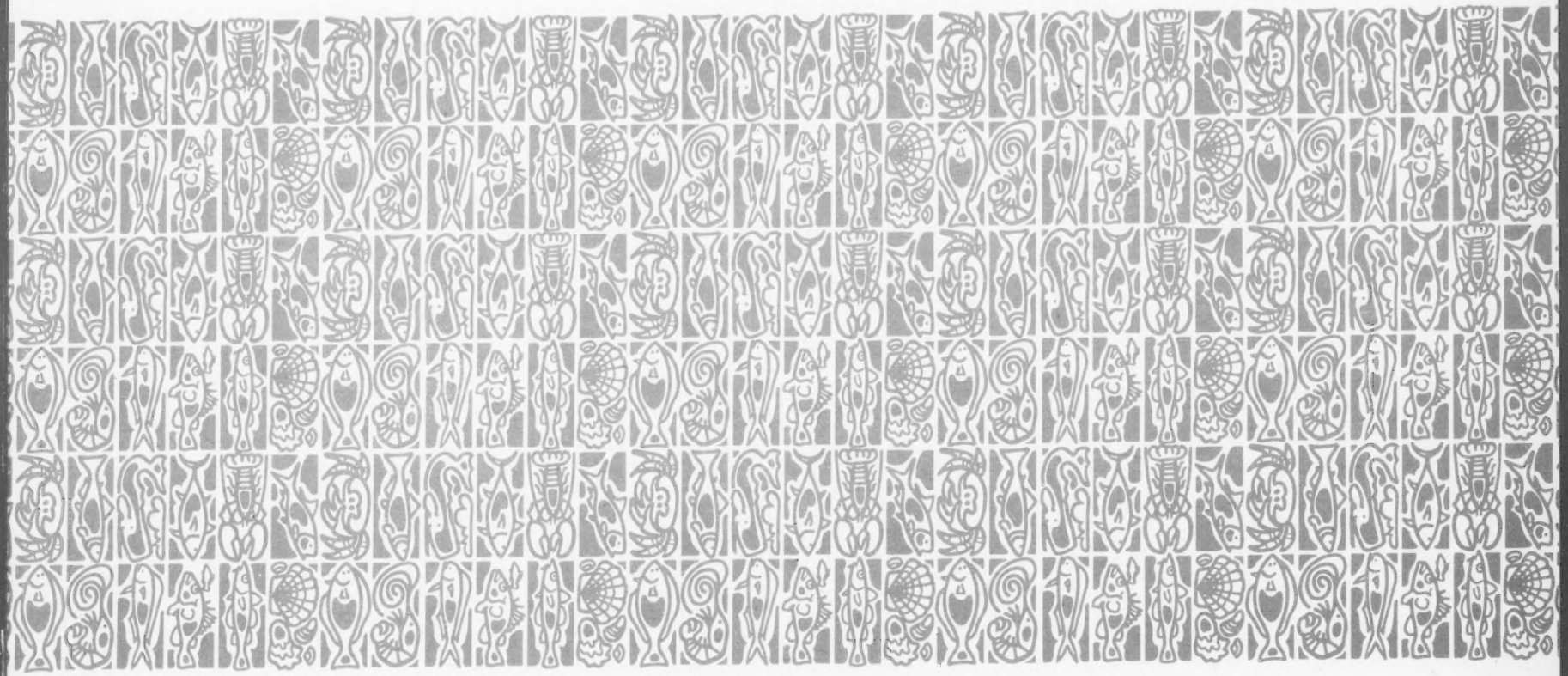
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